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# ILLINOIS BIOLOGICAL MONOGRAPHS

VOLUME XIX

PUBLISHED BY THE UNIVERSITY OF ILLINOIS  
URBANA, ILLINOIS



## CONTENTS OF VOLUME XIX

- Nos. 1-2. The Ostracods of Illinois — Their Biology and Taxonomy.  
By C. CLAYTON HOFF.
- No. 3. The Genus *Conotrachelus* Dejean (Coleoptera, Curculionidae)  
in the North Central United States. By HERBERT FREDERICK  
SCHOOF.
- No. 4. The Embryology of *Larix*. By JAMES MORTON SCHOPF.



# ILLINOIS BIOLOGICAL MONOGRAPHS

Vol. XIX

Nos. 1-2



PUBLISHED BY THE UNIVERSITY OF ILLINOIS  
UNDER THE AUSPICES OF THE GRADUATE SCHOOL  
URBANA, ILLINOIS

## EDITORIAL COMMITTEE

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JOHN THEODORE BUCHHOLZ  
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HARLEY JONES VAN CLEAVE

**THE OSTRACODS OF ILLINOIS**  
**Their Biology and Taxonomy**

**WITH NINE PLATES**

**BY**  
**C. CLAYTON HOFF**

**CONTRIBUTION FROM THE DEPARTMENT OF ZOOLOGY**  
**OF THE UNIVERSITY OF ILLINOIS**

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# CONTENTS

Introduction . . . . .	9
Review of the Literature . . . . .	11
Methods of Collection and Preparation . . . . .	17
Biology of Illinois Ostracods . . . . .	21
Habitats . . . . .	21
Physical Factors in the Habitat . . . . .	25
Biotic Relationships . . . . .	29
Seasonal Distribution . . . . .	33
Reproduction and Ontogeny . . . . .	35
Food . . . . .	38
Geographical Distribution of Ostracods . . . . .	39
Morphology of Fresh-water Ostracods . . . . .	41
Shell . . . . .	41
Body Segmentation and Appendages . . . . .	42
Respiratory, Circulatory, Excretory, Digestive, and Nervous Systems . . . . .	46
Reproductive System . . . . .	48
Taxonomy . . . . .	49
Order Ostracoda . . . . .	49
Suborders of the Order Ostracoda . . . . .	49
Families of the Suborder Podocopa s. str. . . . .	50
Family Cypridae . . . . .	51
Subfamily Candoninae s. str. . . . .	53
Genus Candonia Baird 1845 . . . . .	54
<i>Candonia punctata</i> Furtos 1933 . . . . .	58
<i>Candonia fluviatilis</i> sp. nov. . . . .	60
<i>Candonia simpsoni</i> Sharpe 1897 . . . . .	62
<i>Candonia albicans</i> Brady 1864 . . . . .	67
<i>Candonia biangulata</i> sp. nov. . . . .	70
<i>Candonia recticauda</i> Sharpe 1897 . . . . .	75
<i>Candonia sharpei</i> sp. nov. . . . .	76
<i>Candonia distincta</i> Furtos 1933 . . . . .	77
<i>Candonia crogmaniana</i> Turner 1894 . . . . .	79
<i>Candonia caudata</i> Kaufmann 1900 . . . . .	80
<i>Candonia sigmoides</i> Sharpe 1897 . . . . .	82
<i>Candonia indigena</i> sp. nov. . . . .	85
<i>Candonia suburbana</i> sp. nov. . . . .	88
<i>Candonia fossulensis</i> sp. nov. . . . .	92
<i>Candonia acuta</i> sp. nov. . . . .	96
Subfamily Cyclocyprinae . . . . .	100
Genus Cyclocypris Brady and Norman 1889 . . . . .	101
<i>Cyclocypris forbesi</i> Sharpe 1897 . . . . .	102
<i>Cyclocypris sharpei</i> Furtos 1933 . . . . .	103
Genus Cypria Zenker 1854 . . . . .	104
<i>Cypria turneri</i> sp. nov. . . . .	106
<i>Cypria mediana</i> sp. nov. . . . .	110

<i>Cypria obesa</i> Sharpe 1897 . . . . .	112
<i>Cypria maculata</i> sp. nov. . . . .	114
<i>Cypria ophthalmica</i> (Jurine 1820) Brady and Norman 1889 . . . . .	117
Genus <i>Physocypria</i> Vávra 1897 . . . . .	120
<i>Physocypria pustulosa</i> (Sharpe 1897) G. W. Müller 1912 . . . . .	121
<i>Physocypria dentifera</i> (Sharpe 1897) G. W. Müller 1912 . . . . .	125
Subfamily Ilyocyprinae . . . . .	127
Genus <i>Ilyocypris</i> Brady and Norman 1889 . . . . .	128
<i>Ilyocypris gibba</i> (Ramdohr 1808) Brady and Norman 1889 . . . . .	128
<i>Ilyocypris bradyi</i> Sars 1890 . . . . .	130
Subfamily Cyprinae s. str. . . . .	131
Genus <i>Cypricerus</i> Sars 1895 . . . . .	132
<i>Cypricerus tuberculatus</i> (Sharpe 1908) comb. nov. . . . .	133
<i>Cypricerus fuscatus</i> (Jurine 1820) Sars 1928 . . . . .	135
<i>Cypricerus reticulatus</i> (Zaddach 1844) Sars 1928 . . . . .	139
Genus <i>Cyprinotus</i> Brady 1885 . . . . .	143
<i>Cyprinotus incongruus</i> (Ramdohr 1808) Turner 1895 . . . . .	144
<i>Cyprinotus pellucidus</i> Sharpe 1897 . . . . .	146
Subfamily Notodrominae . . . . .	147
Genus <i>Notodromas</i> Lilljeborg 1853 . . . . .	148
<i>Notodromas monacha</i> (O. F. Müller 1776) Lilljeborg 1853 . . . . .	148
Genus <i>Cyprois</i> Zenker 1854 . . . . .	149
<i>Cyprois marginata</i> (Strauss 1821) Zenker 1854 . . . . .	149
Subfamily Cypridopsinae . . . . .	150
Genus <i>Cypridopsis</i> Brady 1867 . . . . .	151
<i>Cypridopsis vidua</i> (O. F. Müller 1776) Brady 1867 . . . . .	151
Genus <i>Potamocypris</i> Brady 1870 . . . . .	153
<i>Potamocypris smaragdina</i> (Vávra 1891) Daday 1900 . . . . .	154
Family Darwinulidae . . . . .	157
Genus <i>Darwinula</i> Brady and Norman 1889 . . . . .	157
<i>Darwinula stevensoni</i> (Brady and Robertson 1870) Brady and Norman 1889 . . . . .	157
Family Cytheridae . . . . .	159
Subfamily Limnocytherinae . . . . .	160
Genus <i>Limnocythere</i> Brady 1867 . . . . .	160
<i>Limnocythere verrucosa</i> sp. nov. . . . .	161
<i>Limnocythere reticulata</i> Sharpe 1897 . . . . .	163
<i>Limnocythere illinoisensis</i> Sharpe 1897 . . . . .	165
Subfamily Entocytherinae . . . . .	166
Summary . . . . .	167
Bibliography . . . . .	169
Plates . . . . .	175
Index . . . . .	194

## INTRODUCTION

The recent fresh-water ostracods of Illinois, or for that matter of North America, have received relatively little attention from either taxonomists or ecologists. One of the most obvious explanations for the neglect of study of the American fresh-water ostracods undoubtedly has been their relative absence from most open-water plankton samples. Thus they have been delegated little attention from various American investigators who have made detailed studies of other crustaceans such as copepods and cladocerans which are important as plankters in fresh waters. The group has also been overlooked by investigators working on the bottom faunas of American lakes and rivers because the ostracods, being small and active, readily escape from the usual bottom sampling apparatus. Even those investigators concerning themselves with aquatic vegetation and associated animals have often neglected the ostracods, largely perhaps because they were unable to make specific determinations for themselves, and there have been few American authorities to whom material might be submitted for identification. For anyone but the specialist, the specific determination of many of the species has been and still is almost impossible, or at least impractical because the literature is scattered and there are many dissensions in classification and nomenclature. Moreover, it takes considerable time to learn to locate the structures on which specific determination often rests. For these reasons, it is impractical for anyone not especially interested in the taxonomy of ostracods to identify any except the easily recognized species, or species from areas in which a fairly complete survey of the ostracod fauna has been made. The only areas in North America in which fresh-water ostracods have received more than minor consideration are Ohio, Illinois, Massachusetts, Florida, and Washington.

Apparently few investigators have cared to give their attention to an intensive study of ostracods. One reason for this undoubtedly is the difficulty of working in the group. As specific determination usually depends on minute details of the appendages isolated by careful and tedious manipulation, few American investigators have given prolonged attention to the group. Besides the mechanical difficulties encountered, there is a decided deficiency of literature in English, the papers that are available being old or unsuited to open the way readily to anyone desiring to begin work on these forms. Nearly all the more important papers are written in German, and since most of the genera and many of the species are not confined to any one continent, little can be done in the way of taxonomy without consulting these foreign publications.

The stigma of apparent lack of economic or biologic importance has perhaps led many investigators to ignore the ostracods. In contrast to

what is generally thought, however, the ostracods do play an important rôle in the economy of fresh waters. As most species feed on diatoms, bacteria, and minute particles of organic material in the water and are in turn food for many of the larger animals, chiefly fish, they certainly are of some economic significance. Very often, no doubt, a lack of emphasis on ostracods as food for fishes has been the result of an inability to determine taxonomically the species found. In practically all surveys concerned with the availability of food for fishes, the ostracods are identified only to genus, and in some publications all are listed under the blanket term "Cypridae." While it has been well known since the time of Forbes (1888) that many Illinois fishes consume ostracods as a part of their food, the extent to which fish sometimes ingest ostracods is not generally realized. One individual instance of the large numbers of these animals occasionally consumed by fish is shown in an examination of the digestive tract of a single adult individual of *Catostomus commersonii* (Lacépède) from the strip-mine area near Oakwood, Illinois. The ostracods, which completely packed the digestive tract to the exclusion of almost all other kinds of food, included no less than six species, three of which predominated in numbers.

Not only may ostracods be considered economically as potential links in food chains but they are also of interest because often they serve as intermediate hosts for some of the Acanthocephala, especially those which parasitize fish. As an example of an Acanthocephalan life cycle in which an ostracod is the intermediate host is the life cycle of *Neoechinorhynchus cylindratus* (Van Cleave 1913) as worked out by Ward (1940). *N. cylindratus* as an adult parasitizes the large-mouth black bass and has as the first intermediate host *Physocypria globula* Furtos 1933 (= *P. pustulosa* (Sharpe 1897) G. W. Müller 1912). In examining thousands of ostracods mounted on slides, the present writer has found several species infected with Acanthocephala. In material from permanent lakes and streams, the percentage of infection may run from one to one and one-half per cent. While this incidence of infection is not high, it shows the possibilities of securing material for working out life histories in the Acanthocephala. Since many of the primary and secondary intermediate hosts of Acanthocephala are fishes, all stages of the parasite are readily available, and infection experiments may be conducted without great difficulty.

Besides being of distinct economic importance, the ostracods are biologically interesting. Concerning the ostracods in American fresh waters, little is known of the habitats, the factors which govern distribution, or the ecological associations of which they may play an integral part. The present writer has attempted to bring together field data regarding the habitat relationships of the ostracod species of Illinois. The variability shown by various species of ostracods also merits detailed inquiry. The

most noticeable variations are in color, size, and shape of shell and the number and degree of development of tubercles along the shell margin. There is some indication from the field data that the shell color in some species, as *Cypridopsis vidua*, may be correlated with the season and the amount of algae available in the water. Whether or not an abundance of green plant material used as food causes a deepening of the shell color must be determined experimentally. The possible development of races in various local areas is a problem of academic significance. Certain available records of discontinuous variations, such as the number of tubercles along the shell margin in *Physocypria pustulosa*, lend themselves to numerical consideration. Consequently, they may be conveniently used in detecting the presence of isolated races differing from each other in the number of tubercles. Such studies may lead in time to the final settlement of the status of certain questionable species based on differences which are possibly only expressions of individual variation and which appear to the writer to be of less than subspecific importance.

The writer, recognizing the difficulties involved in the identification of ostracods and the lack of knowledge regarding their biology, has attempted herein to make a contribution of such a nature that ecologists, fresh-water biologists, and zoologists in general may have available a workable treatise by which they can, in the first place, identify species occurring in Illinois and, in the second place, gain some insight into the biology of the species found in the state. Paleontologists, who are now giving much attention to the study of fossil forms, may find the information given herein useful in the interpretation of fossil faunas of fresh-water ostracods. It is hoped that the order Ostracoda may continue to be the subject of additional investigation, since direct and detailed information regarding the life histories of most Illinois species is extremely meager, data on the distribution of many species in some parts of the state are entirely wanting, and few physiological and experimental studies have been reported in the literature.

## REVIEW OF THE LITERATURE

*History of Basic European Work on Ostracods.*—The ostracods of North America are little known in comparison with the relative completeness of the knowledge of European forms. Since American workers have followed closely the schemes provided by European writers, a survey of classical European works is considered essential to a study of ostracods indigenous to America. Several comprehensive works have been published on the ostracods of European countries, and complete faunal lists have been very accurately compiled. A comparison of the literature relative to American forms and that concerning European species shows distinctly

that the knowledge of ostracods in America is thirty or forty years behind that in Europe.

The first important publication on ostracods was that of O. F. Müller, in 1785, entitled "*Entomostraca seu Insecta testacea, quae in aquis Daniae et Norvegiae reperit, descripsit et iconibus illustravit.*" Between the beginning and middle of the nineteenth century, several important European papers appeared. These included a work by Jurine in 1820 on the ostracods in the vicinity of Geneva; a doctor's dissertation by Zaddach in 1844 concerning the ostracod fauna of Prussia; and Lilljeborg's publication in 1853 on the ostracod species of Scandinavia. These studies were largely taxonomic in scope. In 1854, Zenker published his "*Monographie der Ostracoden,*" a publication of eighty-seven pages which included not only a taxonomic but also a biologic consideration of the known ostracods. The first important publication in English was written by Brady, appearing in 1868 under the title "*A Monograph of the Recent British Ostracoda.*" With Norman in 1889, Brady published "*A Monograph of the Marine and Freshwater Ostracoda of the North Atlantic and of North-Western Europe. Section I. Podocopa.*" Two years later, Vávra (1891) monographed the ostracods of Bohemia. In 1900, two very important comprehensive papers were published, one by Kaufmann (1900a) on the "*Cypriden und Darwinuliden der Schweiz*" and the other by G. W. Müller under the title "*Deutschlands Süßwasser-Ostracoden.*" Early in the present century, G. W. Müller (1912) brought out his summarizing volume on ostracods as a part of the series "*Das Tierreich.*" Up to the present time, this has remained the only authentic and comprehensive world-wide monograph on the ostracods, and it is still the basic publication for anyone beginning taxonomic work in the group. Among recent monographs of the ostracods of European countries have been those of Alm (1916) on the fresh-water ostracods of Sweden and of Sars (1928) on the ostracods of Norway. More recently Wagler (1937) has published a comprehensive work on European ostracods in his volume on Crustacea in the series entitled "*Die Tierwelt Mitteleuropas,*" and Klie (1938a) has published a monograph on German ostracods in the series "*Die Tierwelt Deutschlands und der angrenzenden Meeressteile.*" While these major publications have been appearing from time to time, there has been an influx into the periodical literature of smaller papers concerned with the taxonomy, morphology, or ecology of a small group of ostracods or the ostracods of a local area.

Comprehensive works on the biology of the ostracods are not so plentiful as those concerned primarily with taxonomy. In many of the taxonomic papers, however, some reference is made to the general biology of the species under consideration. For instance, Zenker's monograph in 1854 included much data of a biological nature as a background for the

taxonomic portion of the publication. Wohlgemuth (1914) and Alm (1916) were among the first to write in detail on the biology of the ostracods of a definite region, Wohlgemuth working on the ostracods of Saxony and Bohemia and Alm on those of Sweden. While G. W. Müller (1927) wrote a general account of ostracods in the Kükenthal-Krumbach "Handbuch der Zoologie," the most complete account of the biology as well as the anatomy and development of fresh-water ostracods is the account by Klie (1926a) in the series "Biologie der Tiere Deutschlands." This publication is applicable to forms from the United States as well as German species, because many of the species from the two countries are identical or closely related.

*History of the Study of American Ostracods.*—Compared with the attention which has been given ostracods by European writers, the meager work by Americans has consisted chiefly of small, scattered papers. With the exception of Klugh's (1927) work on the ecology of a few Canadian species, these papers are chiefly only of taxonomic or zoögeographical importance. The earliest publication on the ostracods of North America is the description by Haldeman (1841) of two new species of "Cypris" from Pennsylvania. The same author (1842a, 1842b) gave descriptions of two more new "Cypris" from Pennsylvania and one from Massachusetts. These ostracods were so inadequately described that their real identity is unknown, and they are listed among the dubious species by G. W. Müller (1912). The best known of early American workers in the field of ostracods are Herrick, Turner, and Sharpe. Herrick published several papers, of which his early ones (1879, 1882) refer in part to the ostracods of Minnesota. In these papers he described a few new species, but in some instances so incompletely that it is impossible now to recognize them. The early deficiency of knowledge of American ostracods is shown by Underwood's publication (1886) of a list of all the described ostracods from America north of Mexico. Here are listed fifteen species, many of which are now considered dubious; none of them were from Illinois. In 1887, Herrick published a list of the fresh-water and marine crustacea of Alabama. This included ten species of ostracods, of which five were described as new. Turner began publishing on ostracods in 1892 and after the appearance of several small publications (1892, 1893, 1894) concerning new species and records, he published in 1895 a work on the "Fresh-water Ostracoda of the United States," which appeared as part three of the "Second Report of the State Zoologist of Minnesota." This publication continued to be the most complete of any on American ostracods until the appearance in 1918 of Sharpe's account in Ward and Whipple's "Fresh-water Biology." Besides Herrick's and Turner's works, a few new species were described by Chambers (1877) and by Forbes (1893) from the western United States.

Shortly after the appearance of Turner's account of the "Fresh-water Ostracoda of the United States," Sharpe (1897) published an account of the ostracods of Illinois which, for his time, excelled in completeness all other state lists. His work was based on a large number of field collections. Sharpe followed this early work by a series of publications (1903, 1908, 1910) based on material collected by himself in Illinois and material from other localities deposited in the United States National Museum. His last publication (1918) was a complete and concise summary of all knowledge of American ostracods up to the time of publication.

Between 1900 and 1933, no monographic studies except that of Sharpe (1918) in Ward and Whipple's "Fresh-water Biology" appeared on American ostracods. Several American workers, however, published short papers. These papers include reports of a few species in Michigan and Nevada by Pearse (1910, 1914); lists from Rhode Island by Williams (1907) and from New Jersey by Fowler (1912); two publications on the ostracods of Massachusetts by Cushman (1905, 1907); and reports of the ostracods from western United States, chiefly Colorado, by Dodds (1908), Cockerell (1912), Blake (1931), and Brues (1932). A notable publication was that of Marshall (1903), in which was described the first *Entocythere* found on the gills of crayfish. During this period from 1900 to 1933, several European workers also studied material from North America. Alm (1914) published an account of the Arctic ostracods of Greenland and part of Canada. Sars, in 1926, gave an account of Canadian ostracods, chiefly from southeastern Canada. Klie (1931a) published an article which included three new species of ostracods from Indiana. In 1914, Weckel compiled a list of all the "free-swimming" ostracods of North America, with keys for their identification.

A new era has begun in the last decade with the publication by Furtos in 1933 of a complete survey of the ostracod fauna of Ohio. She followed this in 1935 by an article on the fresh-water ostracods of Massachusetts and in 1936 by two articles, one (1936a) on ostracods of Florida and North Carolina and another (1936b) on the ostracods from the cenotes of Yucatan and vicinity. More recently, Dobbin (1941) has published a comprehensive survey of the ostracods of the northwest coast region of the United States. At the present time, there are few investigators working on ostracods in the United States, and the field is open for taxonomic and ecological studies, especially those of state-wide significance.

*Reports on the Ostracod Fauna of Illinois.*—Sharpe published the first work on the ostracods of Illinois in 1897. In this publication, Sharpe listed twenty-two species, twelve of which were thought by him to be undescribed. With the exception of two of the reported twenty-two

species, all of them were from Illinois, chiefly from the vicinity of Havana, Mason County, Illinois where the Biological Station of the University of Illinois was located. A few of the twenty species in this initial publication are considered synonyms by the present writer, but seventeen of them are retained as valid. The writer has failed, however, to rediscover five of those listed by Sharpe in this early work.

Sharpe followed his first paper by three others, all of which have some reference to Illinois ostracods. Sharpe's works of 1903 and of 1910 reported little except a few additional references as far as Illinois is concerned, but his publication of 1908 contains the first records of five additional species from Illinois, one of them previously undescribed. Three of these five have not been rediscovered by the present writer. Only three other publications are available with reference to the ostracod fauna of Illinois. One of these is the reference by Kofoed (1908) to several species in the Illinois River at Havana, Illinois. The second is the mention of five species from the Chicago area by Shelford (1913). Neither of these reports contain important new records for the state, but they merit mention here as two of the few instances where ostracods found during the course of an extensive ecological investigation were carefully determined to species. Identification in both of these papers was by Sharpe. The third paper is a publication by the present writer (1942) in which are described two new species of *Entocythere* epizoic on crayfishes from Illinois.

Since the time of Sharpe, no one has published the results of any studies on the free-living ostracods of Illinois. The present writer has, by a study of 713 field collections from sixty-six counties, raised the total of reported free-living species from Illinois to thirty-nine. Of these, thirty-one have been seen by the present writer, while eight were reported by Sharpe but not found during the course of the present investigation. This lack of rediscovery is perhaps the result of two factors: (a) a scarcity resulting from the localized or limited seasonal occurrence of certain species (this is undoubtedly the case with *Cyprois marginata*, which was reported by both Sharpe (1908) and Shelford (1913) from a pond in Jackson Park, Chicago); and (b) an erroneous or incomplete description or one based on abnormal individuals, which has made redetermination impossible. Many of the species not found by the present writer in his collections will certainly be rediscovered when additional collections have been made, since some species are rarely observed, as, for instance, *Darwinula stevensoni* and *Notodromas monacha*, each of which is represented in the present writer's collections by a single individual.

The thirty-nine free-living species reported herein as occurring in Illinois include eleven species described as new to the literature. Seventeen of the thirty-nine species are new records for Illinois.

The following list is a summary of all records concerning free-living ostracods in Illinois.\* In previous reports, species have been recorded often under names which have required some change to bring the nomenclature up to date. For the names used by earlier writers in reporting ostracods from Illinois, the reader is referred to the synonymy under the taxonomic discussion of each species. Here the writers reporting Illinois records are indicated by numbers in parenthesis after the name of each species, as follows: (1) Sharpe 1897; (2) Sharpe 1903; (3) Sharpe 1908; (4) Kofoed 1908; (5) Sharpe 1910; (6) Shelford 1913; (7) the present writer.

Suborder Podocopa *s. str.*

Family Cypridae

Subfamily Candoninae *s. str.*

Genus *Candona* Baird 1845

- C. simpsoni* Sharpe 1897 (1, 4, 7)
- C. punctata* Furtos 1933 (7)
- C. fluvialis* *sp. nov.* (7)
- C. albicans* Brady 1864 (7)
- C. biangulata* *sp. nov.* (1, 7)
- C. crogmaniana* Turner 1894 (7)
- C. sigmoides* Sharpe 1897 (1, 4, 7)
- C. recticauda* Sharpe 1897 (1)
- C. sharpei* *sp. nov.* (1)
- C. caudata* Kaufmann 1900 (7)
- C. distincta* Furtos 1933 (7)
- C. indigena* *sp. nov.* (7)
- C. suburbana* *sp. nov.* (7)
- C. acuta* *sp. nov.* (7)
- C. fossulensis* *sp. nov.* (7)

Subfamily Cyclocyprinae

Genus *Cyclocypris* Brady and Norman 1889

- C. forbesi* Sharpe 1897 (1, 7)
- C. sharpei* Furtos 1933 (3)

Genus *Cypria* Zenker 1854

- C. turneri* *sp. nov.* (1, 4, 6, 7)
- C. mediana* *sp. nov.* (7)
- C. obesa* Sharpe 1897 (1, 5, 7)
- C. maculata* *sp. nov.* (1, 4, 7)
- C. ophthalmica* (Jurine 1820) Brady and Norman 1889 (7)

Genus *Physocypria* Vávra 1897

- P. pustulosa* (Sharpe 1897) G. W. Müller 1912 (1, 4, 7)
- P. dentifera* (Sharpe 1897) G. W. Müller 1912 (3)

Subfamily Ilyocyprinae

Genus *Ilyocypris* Brady and Norman 1889

- I. gibba* (Ramdohr 1808) Brady and Norman 1889 (7)
- I. bradyi* Sars 1890 (7)

Subfamily Cyprinae *s. str.*

Genus *Cypricercus* Sars 1895

- C. tuberculatus* (Sharpe 1908) *comb. nov.* (3, 7)

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\*Two additional species of ostracods, *Entocythere illinoisensis* Hoff 1942 and *E. copiosa* Hoff 1942, have been reported as living in the gill chambers of crayfishes in Illinois (Hoff, 1942). Since these species are epizoid, they are excluded from this list.

- C. fuscatus* (Jurine 1820) Sars 1928 (1, 3, 6)
- C. reticulatus* (Zaddach 1844) Sars 1928 (1, 3, 6, 7)
- Genus *Cyprinotus* Brady 1885
- C. incongruens* (Ramdohr 1808) Turner 1895 (1?) (7)
- C. pellucidus* Sharpe 1897 (1, 2)
- Subfamily Notodrominae
- Genus *Notodromas* Lilljeborg 1853
- N. monacha* (O. F. Müller 1776) Lilljeborg 1853 (3, 6, 7)
- Genus *Cyprois* Zenker 1854
- C. marginata* (Strauss 1821) Zenker 1854 (3, 6)
- Subfamily Cypridopsinae
- Genus *Cypridopsis* Brady 1867
- C. vidua* (O. F. Müller 1776) Brady 1867 (1, 4, 6, 7)
- Genus *Potamocypris* Brady 1870
- P. smaragdina* (Vávra 1891) Daday 1900 (1, 7)
- Family Darwinulidae
- Genus *Darwinula* Brady and Norman 1889
- D. stevensoni* (Brady and Robertson 1870) Brady and Norman 1889 (7)
- Family Cytheridae
- Subfamily Limnocytherinae
- Genus *Limnocythere* Brady 1867
- L. reticulata* Sharpe 1897 (1, 7)
- L. illinoisensis* Sharpe 1897 (1, 4)
- L. verrucosa* sp. nov. (7)

## METHODS OF COLLECTION AND PREPARATION

The material on which this publication is based was collected by the writer during the vernal, aestival, and serotinal seasons of 1940. The collections were made in sixty-six counties of Illinois. An attempt was made to collect impartially. During most of the collecting trips, all available waters were examined, even though the habitat appeared unfavorable for ostracods. In spite of the examination of such uninviting waters, about two-thirds of the samples collected contained one or more species of ostracods. In all, 713 samples from Illinois actually containing ostracods formed the basis for this investigation.

Almost without exception, collections were made with a Birge cone net eleven inches long and four inches in diameter at the open end. The open end is fitted on a sheet-metal cylinder which is closed with a cone of coarse brass wire netting of about three-eighths inch mesh. This cylinder keeps the open end of the net from collapsing and the wire netting prohibits the net from collecting an assortment of vegetation and debris. The organisms are caught in a half-ounce bottle attached to the apex of the net. The entire net with the metal cylinder at the larger end and the collecting bottle at the apex is mounted on a toboggan made of galvanized sheet metal, the cylinder being firmly attached to the sled at the forward end. The collecting bottle lies on the sheet-metal sled and

when in use is held in place by rubber bands fastened through two small holes in the bottom of the sled. This holds the net approximate to the sled at all times and keeps it stretched out in a cone. The adaptation of this apparatus was suggested by the description of the plankton trawl described by Galtsoff (1937). It was found that this net could be dragged on the bottom or through vegetation and roots as well as against rocks without fouling or injury to the net. Samples were made from all kinds of habitats and often several samples were taken from the same general locality in order to include the several available habitats and detect, if possible, any habitat relationships. Each time after using, the net as well as the bottle was washed with as clear water as was obtainable, and from the nature of the samples it is obvious that such washing, even though in the same water from which samples were taken, was effective and individuals were not carried over in the net to contaminate the next sample. In instances where clear open water was not available for washing the net, it was well rinsed just before using in water from which the next collection was to be made.

While quantitative methods are generally recognized as desirable in taking plankton samples, the habitats in which ostracods are to be found preclude the possibility of adapting quantitative methods in the sampling carried on in the present investigation. The cone net is the only apparatus by means of which adequate samples of water could be strained from weedy ponds, algal mats, and the water immediately over mud bottoms where ostracods are abundant. Perhaps following the same historical development as that through which plankton studies in general have gone, the strictly qualitative methods essential in the present survey may be supplemented at a later date by quantitative methods for given habitats or for limited groups of species. At least for the present the writer felt that the infrequency of occurrence of some species in the numerous qualitative samples gives justification for relying on relatively numerous qualitative samples for the initial faunal survey.

At the same time as the samples were taken, a record was made of the date, location, and certain physical factors as the kind of habitat, the force of the current, if any, the nature of the bottom, and the turbidity of the water. In some instances, the hydrogen ion concentration was determined with a LeMotte comparator, using bromthymol blue as an indicator. On making each collection, the associated vegetation was noted in considerable detail in order to learn whether or not there might be a correlation between the presence of certain species of ostracods and the kind of vegetation present. These data were entered in a permanently bound field notebook under a collection number and the date. In the jar containing the sample, there was placed a paper on which was written the date and number of the collection. After examination in the laboratory, all

the collections containing ostracods were given serial numbers and the field data were transferred to notebooks listing each collection by its serial number.

After making the collections by running the net through the vegetation, along the bottom, or on the surface, as the case might be, the sample was poured from the collecting bottle on the net to a four-ounce ointment jar. Collections were usually allowed to accumulate until noon and night, when they were preserved by the addition of 95% ethyl alcohol in an amount equal to the volume of the sample. When the temperature was very high, it was found necessary to preserve the samples more often than twice a day because of the biolytic action of the temperature on some of the organisms. The killing of the ostracods by the addition of an equal volume of 95% ethyl alcohol to the sample is to be recommended. If formalin is added or the animals are dropped into an alcohol of high concentration, many of the animals close the shell tightly, and it is then difficult to remove the valves for examination of the appendages. When killed by adding the alcohol as explained above, the individuals in most species are killed with the shell gaping. If the samples are to be kept for some time before the ostracods are separated from the other material, it is well to raise the concentration of the alcohol to about 85% by pouring off the supernatant alcohol and refilling the jar with a sufficient amount of 95% alcohol. Formalin may be used as a preservative, but the appendages become stiffened and dissection is made more difficult. Care must also be taken in the use of commercial formalin, since much of the commercial solution is not acid-free, and the samples will gradually deteriorate through decalcification of the shells.

After sorting out the material in the collections, representatives of the species in each sample were usually mounted permanently for study. This was necessary for the checking of the identification of many of the species, although it did involve considerable labor and materials. Even though a few common species such as *Cypridopsis vidua* and *Potamocypris smaragdina* are recognizable under the binocular dissecting microscope, the writer made a series of slides of such common forms in order to verify the identification and discover, if possible, whether or not races occur in different localities. While it may seem a waste of energy to mount hundreds of individuals of common and easily recognized species, it is the only way in which limits of the variation of a species can be determined. By knowing the limits of variation, one may avoid describing as new the ultimate ends of a series representing a single species.

Two methods were used in making slides. It was found that glycerine mounts were convenient and these were used in some instances. A slide is ringed with several layers of gold size or asphaltum and the ostracod, after being cleared in glycerine, is dissected in a drop of glycerine on the

slide within the ring. A cover slip is then placed over the dissection and sealed with material similar to that used in making the initial ring. While this is a rapid way of making slides and shows the finer structural details to good advantage, it has several disadvantages. Among these might be mentioned the poor preservation of material and lack of permanency in contrast to mounting media such as diaphane or balsam; the lack of any staining to bring out certain structures; and the impossibility of mounting most shells in this way because of their size. This last makes necessary a separate mounting of shells in some other medium under a second cover to the side of the glycerine mount. Since the mounting of the shell is necessary to keep shell and soft parts together and avoid loss of the former, and since in this method of mounting, the shell has to be dehydrated for mounting in balsam or diaphane, it is just as convenient to dehydrate the entire animal and mount in some one of the more nearly permanent media.

The most satisfactory mounts of ostracods are made by staining with acid fuchsin. The ostracods are removed from the preserving alcohol and placed in a LeFevre embryological watch glass in which they are run through lessening concentrations of alcohol to water. They are then washed in a small amount of 1/50-N solution of hydrochloric acid for about one minute. After pipetting off the acid water, a 0.5% aqueous solution of acid fuchsin is placed in the watch glass and the animals are allowed to remain in this stain from one to five hours depending on the species and perhaps, to a larger degree, on the recency of molting, since newly molted ostracods seem to stain more favorably than the exuviae or animals long molted. After staining, the acid fuchsin solution is removed with a pipette and the material washed rapidly several times in a 1/50-N solution of hydrochloric acid. The hydrochloric acid solution appears to intensify the stain. Overstaining seldom occurs, but destaining, if necessary, may be carried out by washing the material in alkaline tap water or slightly alkalized alcohol. The material, after washing in acid water, is run through the alcohol series to absolute alcohol. Since the alcohol is pipetted off after each treatment and the watch glass retains a small amount of the solution, it is well to wash at least twice with alcohols of each grade, especially of the higher concentrations. If mounting is to be done in balsam, the material dehydrated in alcohol is cleared in xylol (at least three changes). The cleared animal is placed in a drop of balsam on a slide under the binocular and the shell removed by the use of fine needles. The shell halves are removed to a second drop of balsam on the same slide and covered by a slip supported by bits of broken glass or pieces of capillary tubing of the appropriate diameter. The appendages are then isolated in the first drop of balsam and a cover slip added without any support, since it is necessary to have a thin mount in which

the appendages are extended as much as possible in one plane. By leaving the cover unsupported, it is possible to use an oil immersion lens for the observation of fine setae and serrations. As the shells and soft parts take up but little room on the slide, it is often possible to use circular cover slips only one-fourth of an inch in diameter. If more than one animal is mounted under a single slip, it may be necessary to employ larger covers.

A more successful mounting method has been the bringing of stained material into diaphane directly from absolute alcohol. The principal advantage of this procedure is the elimination of one of the steps, that of clearing, thus saving time and materials and avoiding the hardening action of the clearing fluid. The dissection of material which has not passed through any of the usual clearing fluids is more easily accomplished than it is in material cleared in such fluids. The diaphane clears the material sufficiently for good observation, a partial clearing really being much more adequate than clearing in xylol or some other clearing reagent in which the animals become so transparent that some of the finer structures cannot be clearly observed. In mounting in diaphane from absolute alcohol, care must be taken to use several changes of the alcohol in order to completely dehydrate the material. To avoid the passing of alcohol into the diaphane, the material should be placed on the end of a slide in as small a drop of alcohol as possible and the alcohol removed by absorption with a small piece of filter paper. The animal is then transferred to the diaphane with a needle. Dissection may be carried out just as in balsam-mounted ostracods, and the valves, if large, are mounted under a separate cover. Sometimes it is advantageous to keep the soft parts intact after removal from the shell in order to be able to orient properly the various parts of the animal.

## BIOLOGY OF ILLINOIS OSTRACODS

### HABITATS

If sufficient search is made, there will be found scarcely a single kind of aquatic habitat in which ostracods are not found. Since the state of Illinois is entirely an inland state, no mention need be made here to the biology of the ostracods living in brackish or marine waters.

The habitats investigated by the present writer include many kinds of still and running waters. These have been grouped for convenience into four types: (1) temporary still waters, including all vernal or temporary ponds whether old ox-bows, prairie and forest pools, roadside ditches, or small water-filled depressions; (2) permanent still waters, including lakes both artificial and natural, swamps which do not dry up

during the aestival or serotinal seasons, and the lake-like backwaters of large rivers; (3) temporary running waters and the pools left in stream beds after the stream has ceased to flow; and (4) permanent streams of all sizes. Each one of these habitats presents a variety of ostracod species, but the running waters have fewer species than the still waters. The only habitat investigated by the writer in which large numbers of several species did not occur were the waters extremely high in organic material such as some of the cypress swamps in southern Illinois.

Certain habitats have not been investigated because of lack of time and facilities. No attempt was made to explore the ostracod fauna of Lake Michigan, since the lake presents certain problems which make it somewhat separate from the remainder of the state as far as the collector is concerned. It was also impossible to visit tamarack bogs in the northern part of the state since these have been closed to the public. A habitat which will no doubt prove fruitful when investigated is that of underground waters. A large number of species, chiefly of the genus *Candona*, have been described from wells, springs, and cave waters in Europe by Kiefer and Klie (1927), Klie (1934, 1936, etc.), and others. That possibilities are present in Illinois for a study of subterranean species is shown by the report of Klie (1931a) of some species from the waters in an Indiana cave. The water of crayfish burrows also merits examination. Creaser (1931) reported *Cypria exsculpta* (? = *Cypria turneri* sp. nov.) abundant in the burrows of the crayfish *Cambarus diogenes* in Missouri, and the present writer has taken a few species of ostracods from a similar habitat in Illinois.

After a detailed survey of the various species of ostracods, it was found that certain species could be classified as occurring in temporary or permanent and still or running waters. The minor subdivisions of the four types of habitat already suggested have no significance as far as the biology of the ostracods is concerned; and, indeed, the kinds of associations in a given habitat seem to limit but little the distribution of particular species. Thus the same species may be found along the margin of a large lake regardless of whether the sample is taken in masses of algae, decaying grass, different species of aquatic spermatophytes, or even from bottom practically devoid of vegetation. In the same manner, the species found in a small stream usually vary little whether taken from masses of algae or in mats of plants or whether the collection is made in a quiet pool or in an area where the water is flowing. The sum total of the factors which are found expressed in the four types of habitats listed appears to determine to a large degree, and with few exceptions, the species of ostracods present. Thus the independent factors such as type of bottom, current, and associated vegetation determine only to a minor degree the distribution of most species.

TABLE 1

Table showing the incidence, expressed in percentages, of each species observed by the writer in temporary and permanent, still and running waters. The name of each species is followed by the number of collections in which it occurred.

Species	Collections	Still waters		Running waters	
		Temp.	Perm.	Temp.	Perm.
<i>Candona distincta</i> .....	3	100	..	..	..
<i>Candona indigena</i> .....	4	100	..	..	..
<i>Candona suburbana</i> .....	2	100	..	..	..
<i>Candona fossulensis</i> .....	2	100	..	..	..
<i>Cypria ophthalmica</i> .....	9	44	56	..	..
<i>Cypricercus reticulatus</i> .....	31	87	..	13	..
<i>Candona biangulata</i> .....	4	50	..	50	..
<i>Candona albicans</i> .....	4	25	..	75	..
<i>Cypria turneri</i> .....	29	48	38	7	7
<i>Candona simpsoni</i> .....	83	39	26	23	12
<i>Cypria obesa</i> .....	9	33	45	11	11
<i>Cypridopsis vidua</i> .....	505	20	48	10	22
<i>Limnocythere reticulata</i> .....	69	16	2	54	28
<i>Cyprinotus incongruens</i> .....	16	13	6	44	37
<i>Cypria maculata</i> .....	43	12	42	9	37
<i>Physocypria pustulosa</i> .....	175	8	78	4	10
<i>Potamocypris smaragdina</i> .....	118	6	41	11	42
<i>Ilyocypris gibba</i> .....	44	4	2	49	45
<i>Ilyocypris bradyi</i> .....	71	1	4	47	48
<i>Limnocythere verrucosa</i> .....	4	..	100	..	..
<i>Darwinula stevensoni</i> .....	1	..	100	..	..
<i>Notodromas monacha</i> .....	1	..	100	..	..
<i>Cypricercus tuberculatus</i> .....	3	..	100	..	..
<i>Cyclocypris forbesi</i> .....	1	..	100	..	..
<i>Candona crogmaniana</i> .....	2	..	100	..	..
<i>Cypria mediana</i> .....	3	..	33	67	..
<i>Candona caudata</i> .....	3	..	33	33	33
<i>Candona punctata</i> .....	1	..	..	100	..
<i>Candona fluviatilis</i> .....	3	..	..	100	..
<i>Candona acuta</i> .....	5	..	..	80	20
<i>Candona sigmoides</i> .....	4	..	..	..	100

The frequency with which ostracods may be collected without regard to bottom or vegetation throughout a given pond, lake, or stream may be shown by the following two examples taken from many similar instances in the writer's data:

(1) On June 4, 1940, four samples were taken from Twin Lakes at Paris, Edgar County, Illinois. One sample was made from a mass of old leaves in water eight inches deep over a mud bottom where there was no aquatic vegetation or algae; a second collection was made in water of about the same depth where there were many aquatic plants and considerable algae; a third sample was taken above a rock bottom in mixed algae and decaying vegetation; and the last was a surface sample where the water was two feet deep. Each of the four samples contained the following three species: *Cypridopsis vidua*, *Potamocypris smaragdina*, and *Physocypria pustulosa*.

(2) In three samples taken from a drainage ditch near Rantoul, Champaign County, Illinois, on June 20, 1940, *Limnocythere reticulata* was found abundant. The samples were taken as follows: the first from a backwater area with decaying corn stalks over a silt bottom; the second from along the edge of the stream in grass overhanging the mud bank where there was some current; and the third was from masses of algae clinging to the gravel bottom of a pool under the highway bridge.

While the distribution in any habitat of most of the species present is very general, some species, as many *Candona* species, are sometimes found isolated in definite regions. No logical excuse for such localization has appeared in the writer's data. A detection of many of the minor environmental factors which play a rôle in distribution probably will be discovered only by detailed laboratory experimentation. It is safe, however, to state that in general the more common species are limited in their habitat range only by the generalized conditions expressed in still temporary waters, permanent still waters, temporary running waters, and permanent running waters or by much finer analysis of environmental conditions than has even been possible in field studies. The distribution of species according to the type of habitat is shown in Table 1. By reference to the table, it will be seen that there are certain species apparently characteristic of each of the four types of habitats, others which occur in combinations of two or three habitats, and some that are found in all the types of habitats. While there is a fair degree of consistency in habitat relations for many of the species, the association is not absolute. In the same manner that species serve as index organisms in other biological phenomena, these species are not always immutable indices to specific habitat conditions. The kinds of habitats or combination of habitats with the characteristic ostracod species\* of each may be listed as follows:

- (1) Ostracods chiefly of vernal ponds:
 

<i>Candona distincta</i>	<i>Candona fossulensis</i>
<i>Candona indigena</i>	<i>Cypricercus reticulatus</i> (usually)
<i>Candona suburbana</i>	
- (2) Ostracods chiefly of permanent lakes:
 

<i>Candona crogmaniana</i>	<i>Notodromas monacha</i>
<i>Cyclocypris forbesi</i>	<i>Darwinula stevensoni</i>
<i>Physocypria pustulosa</i> (usually)	<i>Limnocythere verrucosa</i>
<i>Cypricercus tuberculatus</i>	
- (3) Ostracods typical of temporary streams:
 

<i>Candona punctata</i>	<i>Candona fluviatilis</i>
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- (4) Ostracods typical of permanent running waters:
 

<i>Candona sigmoides</i>	
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- (5) Ostracods found in both temporary and permanent still waters:
 

<i>Cypria ophthalmica</i>	
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\*Because of the incompleteness of the data of former workers, only those ostracods are shown here that were actually observed by the writer in the course of his field work. What is known regarding the ecology of any other species recorded for Illinois may be found under the species description.

- (6) Ostracods collected chiefly in both temporary and permanent running waters:

<i>Candona acuta</i>	<i>Cyprinotus incongruens</i>
<i>Ilyocypris bradyi</i>	<i>Limnocythere reticulata</i>
<i>Ilyocypris gibba</i>	

- (7) Ostracods found in temporary still and running waters:

<i>Candona albicans</i>	<i>Candona biangulata</i>
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- (8) Species found in three or more kinds of habitats:

<i>Candona simpsoni</i>	<i>Cypria obesa</i>
<i>Candona caudata</i>	<i>Cypria maculata</i>
<i>Cypria turneri</i>	<i>Cypridopsis vidua</i>
<i>Cypria mediana</i>	<i>Potamocypria smaragdina</i>

Except for the species which have been taken in but one or two collections, little change in the knowledge of the habitat of any species should be effected by additional collections. At the same time, many of the records based on a single sample are no doubt accurate, since they represent species which are known to be limited in their range of habitat.

#### PHYSICAL FACTORS IN THE HABITAT

While the distribution of ostracods appears to be limited grossly by the type of habitat rather than certain single isolated environmental factors, there is a slight correlation between some of the physical factors and the occurrence of certain ostracod species. According to P. R. Needham (1938), there are five physical conditions which largely determine the distribution of aquatic organisms. These are (1) type of bottom; (2) velocity of current; (3) depth of water; (4) temperature of water; (5) materials in suspension and solution. Of these factors, two were recorded in considerable detail in the field notes. These were (1) type of bottom and (2) the amount of current. Since most of the collections were made from shallow ponds and streams and from the littoral zone of the larger bodies of water, the depth showed no distinguishable effect on the distribution. Roughly speaking, the writer's experiences in the field seem to indicate that the limited temperature ranges found in Illinois also have little effect on the distribution of species of ostracods. Although some species are inhabitants of cool vernal ponds or the larger, cooler lakes of northern Illinois, there seems to be, offhand, no indication that water temperature is in any way causal to the distribution of ostracod species. The effect of temperature on the life cycle and activities of ostracods can, perhaps, best be approached from an experimental point of view before any definitive effect can be ascertained under natural conditions. As a result of the limited time allowed for this study and the difficulty of carrying and using elaborate apparatus which would have hindered the rapidity necessary for collection of a large number of field samples, no effort was made to test the turbidity of the water or to determine the materials in solution. The hydrogen ion concentration,

however, was determined on about one-fourth of the samples secured. No more tests were made since, as a rule, the waters of the northern two-thirds of the state are alkaline. A number of tests were made to check the character of the water in the southern portion of the state where it is often acid especially in Franklin, Johnson, and Massac Counties.

*Kind of Bottom.*—In regard to the effect of the type of bottom on the occurrence of ostracods, no very definite correlation has been found in most species, and the distribution appears usually to be random as far as the type of bottom is concerned. As the proportionate number of times in which a species was found associated with different types of substratum was usually about the same as the number of times samples were taken from the same type of substratum, no correlation between range and type of bottom is evident in most cases. Many of the *Candona* species show a slight correlation with the type of bottom, a more-than-average number of collections being made on a mud bottom for many of the species. This is related, no doubt, to the occurrence of many *Candona* species in temporary waters where mud is usually the substratum encountered. Besides, most of the *Candoninae* crawl on the bottom, and mud is more favorable for animals of such a habit than is a sand bottom. Three species besides those of the genus *Candona* show a tendency to be associated with a particular type of bottom. These species are listed below with the percentages of incidence over various substrata along with the percentage for comparison of each type of substratum in the total number of collections.

	Mud	Hard clay	Sand and gravel	Rock
<i>Cypricercus reticulatus</i> .....	100%	0%	0%	0%
<i>Cyprinotus incongruens</i> .....	59	0	35	6
<i>Potamocypris smaragdina</i> .....	49	5	36	10
Average of all collections.....	73	4	19	5

Since all thirty-two of the collections of *Cypricercus reticulatus* were found over a mud bottom, it is obvious that this species is somewhat similar to the *Candona* species already mentioned. Like many of the *Candoninae*, this species is an inhabitant of temporary waters. Why there should be an increase over the average of incidence in the case of *Cyprinotus incongruens* on a sandy bottom is not known, but in the case of *Potamocypris smaragdina* the increase of a sand and gravel bottom as a substratum may be the result of this species occurring in great abundance in permanent waters where sand and gravel shores are common. Hence the type of bottom is a limiting factor in very few species but rather an incidental factor related to the habitat in general.

*Current.*—In contrast to the relegation of the type of bottom to a minor position as a factor in the distribution of ostracods, there is a marked relationship between the velocity (as measured by inspection

TABLE 2

Table showing incidence, expressed in percentages, of each species observed by the writer in varying conditions of current. The name of each species is followed by the number of collections in which it occurred.

Species	Collections	No current	Little current	Much current	Swift current
<i>Candona punctata</i> .....	1	100	..	..	..
<i>Candona crogmaniana</i> .....	2	100	..	..	..
<i>Candona distincta</i> .....	3	100	..	..	..
<i>Candona indigena</i> .....	4	100	..	..	..
<i>Candona suburbana</i> .....	2	100	..	..	..
<i>Candona fossulensis</i> .....	2	100	..	..	..
<i>Cyclocypris forbesi</i> .....	1	100	..	..	..
<i>Cypria mediana</i> .....	3	100	..	..	..
<i>Cypria ophthalmica</i> .....	8	100	..	..	..
<i>Cypricercus tuberculatus</i> .....	3	100	..	..	..
<i>Notodromas monacha</i> .....	1	100	..	..	..
<i>Darwinula stevensoni</i> .....	1	100	..	..	..
<i>Limnocythere verrucosa</i> .....	4	100	..	..	..
<i>Cypria obesa</i> .....	9	78	22	..	..
<i>Candona biangulata</i> .....	5	60	40	..	..
<i>Candona albicans</i> .....	4	75	..	25	..
<i>Candona caudata</i> .....	3	67	..	33	..
<i>Cypria turneri</i> .....	28	94	3	3	..
<i>Physocypris pustulosa</i> .....	172	92	7	1	..
<i>Cypricercus reticulatus</i> .....	30	90	7	3	..
<i>Cypria maculata</i> .....	42	64	24	12	..
<i>Cyprinotus incongruens</i> .....	16	31	38	31	..
<i>Cypridopsis vidua</i> .....	500	80	16	3	1
<i>Candona simpsoni</i> .....	84	79	14	5	2
<i>Potamocypris smaragdina</i> .....	117	68	30	1	1
<i>Limnocythere reticulata</i> .....	70	50	26	20	4
<i>Ilyocypris gibba</i> .....	42	27	48	18	7
<i>Ilyocypris bradyi</i> .....	72	26	44	24	6
<i>Candona aanta</i> .....	5	20	40	20	20
<i>Candona fluvialis</i> .....	3	..	100	..	..
<i>Candona sigmoides</i> .....	4	..	50	25	25

only) of the flow or the absence of current and certain ostracod species. From Table 2 it may be observed that while most of the species investigated are abundant in quiet water, many of these same species tolerate varying rates of flow. Certain species, however, are confined almost without exception to water in which there is no current. Although the number of collections of most *Candona* species are relatively few, there is considerable evidence that the following species are chiefly confined to quiet waters: *C. crogmaniana*, *C. distincta*, *C. indigena*, *C. suburbana*, and *C. fossulensis*. Three species of *Cypria*, *C. turneri*, *C. mediana*, and *C. ophthalmica*, belong also in habitats in which there is no current. *Cypricercus tuberculatus*, *Notodromas monacha*, *Darwinula stevensoni*, and *Limnocythere verrucosa* have been taken only from the still waters of northern lakes. Two common species, *Physocypris pustulosa* and *Cypricercus reticulatus*, are seldom taken from flowing waters. Areas which are

subject to considerable wave action appear to be no different as far as the ostracods are concerned than areas of quiet water. This is easily conceivable since many of the ostracods live in the plant zone where the action of the waves is not pronounced.

While certain species of ostracods are found usually in quiet waters, other species occur more abundantly in flowing waters. *Candona fluviatilis*, *C. sigmoides*, and *C. acuta* are common in running water, the last two species sometimes being found where the flow is swift. Among the species most typical of streams are *Ilyocypris gibba*, *I. bradyi*, *Cyprinotus incongruens*, and to some extent *Limnocythere reticulata*. A few species which are usually found in still water, are frequent also in a little current and some may even tolerate swiftly flowing water at times, especially during flooded conditions. Two of these, *Cypridopsis vidua* and *Potamocypris smaragdina*, sometimes are found in rapidly flowing water, although they are more abundant where there is no current.

The velocity of flow is no doubt a limiting factor in the distribution of many ostracod species. Many of the forms living in areas where considerable current is found are adapted by having the antennae modified for creeping rather than swimming. A rather large shell, rectangular, compressed, and sometimes ornamented by furrows or protuberances seems to be characteristic of species living in running waters. On the other hand, active swimmers as most of the Cypria species, *Cypridopsis vidua*, *Physocypria pustulosa*, and *Potamocypris smaragdina* seem adapted to quiet water, since they have well developed swimming setae, often tumid shells, and have little ability to maintain themselves against strong currents.

*Hydrogen Ion Concentration.*—The only other physical factor given consideration in the field was the hydrogen ion concentration. Most species do not appear to tolerate waters which are strongly acid in reaction. This is especially true of the species with large, heavily calcified shells. Such forms, as many of the *Candona* species, *Cyprinotus incongruens*, and the two Illinois species of *Ilyocypris* are included in this group. On the other hand, many of the Cypria species tolerate acid conditions, and these include for the most part species which have small shells apparently protected by a heavy organic covering as evidenced by color and texture. Many of the Cypria forms as well as *Physocypria pustulosa* and *Cypridopsis vidua* fall into this group. Because of the acid nature of the water in the extreme southern part of Illinois, the writer believes that the absence there of many species elsewhere common may be explained on the basis of their intolerance to the acid environment. Two species of Cypria, *C. mediana* and *C. ophthalmica*, are, on the other hand, absent from the northern half of the state, and since they are forms which tolerate an acid condition, it is possible that the conditions are not

proper for their continued propagation in the highly alkaline lakes of northern Illinois.

It is regrettable that data relative to other physical factors could not have been collected for analysis, but this was impossible with the limited time available. As a result, however, it is possible to state that, on the basis of the data at hand, there are certain species of ostracods confined more or less to definite habitats and that in general the distribution of ostracods is limited, to some extent at least, by the velocity of the current and the hydrogen ion concentration of the water. Other physical factors, such as the nature of the bottom, appear to have little to do with habitat selection.

#### BIOTIC RELATIONSHIPS

At the beginning of this investigation, the writer held the preconceived idea that there might be species of ostracods characteristic of different plant associations and species which might be commonly associated together. The data collected in the field failed to verify either of these ideas. A few species show higher incidence, however, on bare bottom or as a constituent of plankton than do other species.

As mentioned in the introduction, ostracods are not important as plankters, in spite of the statement by Welch (1935) to the contrary. Some species, it is true, are occasionally found in open water plankton samples (Table 3), but they are of such minor importance that they are not mentioned by Eddy (1934) in his study of fresh-water plankton communities. Kofoid (1908), in one of the most intensive surveys ever made on the plankton of a river system, lists a few species found in plankton from the Illinois River at Havana, Illinois. He found *Candona simpsoni* "occasionally adventitious" in plankton samples. This is rather peculiar as the *Candona* species are not very natatorial, since they lack swimming setae on the antennae. Kofoid's record of this species in plankton is substantiated by the records of the present writer who has found the same species occurring as a plankter. Kofoid also reported *Cypria ophthalmica* and *Cypridopsis vidua* as common and *Cypria exsculpta* (= *Cypria turneri*) and *Cypria pustulosa* (= *Physocypria pustulosa*) as rare in plankton. He also collected a typical bottom form, *Limnocythere reticulata*, in the plankton at the time of flood waters. *Cypria turneri* and *Physocypria pustulosa* reached the highest incidence of all those species found in plankton in the writer's samples. Of these, the first was taken as a plankter in seven per cent and the second in six per cent of the samples in which they occurred. *Cypria maculata*, *Cypridopsis vidua*, *Potamocypris smaragdina*, and *Candona simpsoni* may also be taken occasionally in areas of open water. It will be noticed that the ostracod species found in plankton are, more often than not, active

TABLE 3

Table showing the incidence, expressed in percentages, of certain species found in collections from bare bottom areas, in plankton, and associated with different kinds of vegetation. The name of each species is followed by the number of collections in which it occurred. (Aqua. vege. = Aquatic vegetation (Spermatophytes); Dec. vege. = Decaying vegetation.)

Species	Collections	Bare bottom	Grass	Aqua. vege.	Alga	Dec. vege.	Plankton
<i>Candona biangulata</i> . . . . .	5	60	40	..	..	..	..
<i>Cyprinotus incongruens</i> . . . . .	18	11	39	..	50	..	..
<i>Cypria obesa</i> . . . . .	11	9	37	36	18	..	..
<i>Cypria ophthalmica</i> . . . . .	10	10	40	..	30	20	..
<i>Ilyocypris gibba</i> . . . . .	47	15	42	6	28	9	..
<i>Ilyocypris bradyi</i> . . . . .	77	10	35	13	29	13	..
<i>Limnocythere reticulata</i> . . . . .	79	8	35	10	27	20	..
<i>Cypria turneri</i> . . . . .	29	14	31	14	17	17	7
<i>Physocypris pustulosa</i> . . . . .	188	8	19	30	31	6	6
<i>Candona simpsoni</i> . . . . .	93	6	44	10	29	9	2
<i>Cypridopsis vidua</i> . . . . .	537	4	30	24	30	9	3
<i>Cypria maculata</i> . . . . .	48	2	32	20	40	2	4
<i>Potamocypris smaragdina</i> . . . . .	126	2	21	29	40	6	2
<i>Candona albicans</i> . . . . .	6	..	50	..	50	..	..
<i>Cypricercus reticulatus</i> . . . . .	32	..	50	..	16	34	..
<i>Candona acuta</i> . . . . .	5	..	20	20	20	40	..

swimmers with a small and plump shell. Certainly they do not breed in open water and are, as Kofoid states (1908), completely adventitious in plankton, since they are apparently derived from vegetation-covered areas near shore or in backwater lakes.

*Candona biangulata* appears to be the only ostracod found in the majority of instances on bare bottom. The factor responsible for this trait cannot, at present, be determined but may be related to food habits about which little is known. In general, the association of most species with different types of vegetation deviates little from the average for all the collections. A very limited number of species are absent from associations dominated by aquatic plants. These include *Candona albicans*, *C. biangulata*, *Cypria ophthalmica*, *Cypricercus reticulatus*, and *Cyprinotus incongruens*. This lack of average incidence of association with aquatic spermatophytes may be explained in some instances by the fact that *Candona albicans*, *C. biangulata*, and *Cypricercus reticulatus* are inhabitants only of temporary waters and as a result do not have occasion to become associated with aquatic seed plants which reach a high degree of development in permanent waters. In the same way, it is possible that *Cyprinotus incongruens* has little opportunity for more than mere chance association with such plants, since it is chiefly an inhabitant of running waters where water plants are not abundant. It is difficult, however, to

explain the absence of *Cypria ophthalmica* from the aquatic vegetation since it is entirely a species of still waters, both temporary and permanent. However it is unsafe to venture the opinion that the presence of aquatic vegetation limits the distribution, since the number of samples in the case of *C. ophthalmica* is relatively small and the range of this species does not include northern Illinois, where a majority of the collections from aquatic vegetation was made. It appears then that there is no conspicuous relationship or specific association between certain species of ostracods and certain types of vegetation other than what might be legitimately expected as incident correlations resulting from reflections of the general habitat and range of the species.

The writer gave special attention to the ostracods taken from growths of various species of aquatic plants especially in the lakes of Lake and Cook Counties in an effort to determine if any relationships existed between certain species of ostracods and specific water plants. Most of the collections used for this particular part of the study were made by Bertrand A. Wright who supplied the identification of the plants. A few examples of this type of data, showing the plants present where various ostracods were found may be assembled as follows:

(1) West Loon Lake, Lake County, Illinois; August 7, 1940:

<i>Potamocypris smaragdina</i> .....	} <i>Chara sp.</i>
<i>Cypridopsis vidua</i> .....	
<i>Limnocythere verrucosa</i> .....	} <i>Chara sp.</i>
<i>Potamocypris smaragdina</i> .....	
<i>Cypridopsis vidua</i> .....	
<i>Limnocythere verrucosa</i> .....	} <i>Chara sp.</i> and <i>Potamogeton natans</i>
<i>Potamocypris smaragdina</i> .....	
<i>Cypridopsis vidua</i> .....	
<i>Potamocypris smaragdina</i> .....	} <i>Vallisneria sp.</i>
<i>Limnocythere verrucosa</i> .....	
<i>Potamocypris smaragdina</i> .....	} <i>Potamogeton crispus</i> and <i>P. natans</i>
<i>Cypridopsis vidua</i> .....	
<i>Potamocypris smaragdina</i> .....	} <i>Chara sp.</i> and alga
<i>Limnocythere verrucosa</i> .....	

(2) East Loon Lake, Lake County, Illinois; August 7, 1940:

<i>Potamocypris smaragdina</i> .....	} <i>Chara sp.</i> and <i>Potamogeton natans</i>
<i>Cypridopsis vidua</i> .....	
<i>Potamocypris smaragdina</i> .....	} <i>Ceratophyllum sp.</i>
<i>Cypridopsis vidua</i> .....	
<i>Physocypria pustulosa</i> .....	} White water lily and <i>Myriophyllum sp.</i>
<i>Cypridopsis vidua</i> .....	
<i>Cypridopsis vidua</i> .....	<i>Spirogyra sp.</i>
<i>Potamocypris smaragdina</i> .....	} <i>Chara sp.</i> , <i>Myriophyllum sp.</i> , and <i>Potamogeton sp.</i>
<i>Cyclocypris forbesi</i> .....	
<i>Cypridopsis vidua</i> .....	

*Potamocypris smaragdina*..... } *Potamogeton crispus* and *Chara* sp.  
*Cypridopsis vidua*..... }

(3) Lake at strip-mine area, Vermilion County, Illinois; September 19, 1940:

*Cypridopsis vidua*..... } Alga and Sago weed  
*Potamocypris smaragdina*..... }  
*Cypridopsis vidua*..... *Dianthera americana*  
*Cypridopsis vidua*..... Sargasso weed  
*Cypridopsis vidua*..... *Ceratophyllum* sp.

These data illustrate admirably the condition found in lakes in general. The ostracod species show no distinct favoritism for certain plants and appear not to be a part of any particular association. It will be seen that in only two instances are there species in a given collection that do not occur in several other collections from the same lake on the same date. For one of these, *Cyclocypris forbesi* from East Loon Lake, this is the only time it was taken during the entire field investigation and so has little significance here, since its occurrence in the state is rare. Likewise, the presence of *Potamocypris smaragdina* in the strip-mine lake is probably insignificant as far as associations are concerned, since it is found associated with all kinds of plants in both East and West Loon Lakes.

An examination of the data was also made to determine if the species of ostracods formed associations among themselves. It was thought by the writer that such information might be useful in proving that there are certain environmental factors which govern the distribution of ostracod species. If it were possible to show that certain species of ostracods were always associated together, it would be sound evidence that environmental factors limited the distribution of groups of species reacting similarly to the same limiting factors. A close study of the incidence, in which certain species occurred together, showed no significant correlation indicative of any inter-group associations. The data are too bulky to give in detail here and too insignificant to merit detailed discussion. Apparently association of two or more species is largely by chance, except as such associations are made up of species which are characteristic of one of the four kinds of habitats already described. Thus *Ilyocypris* spp. and *Limnocythere reticulata* are often found associated together in running water.

As an incidental observation, the writer found that protective coloration appears to be well developed in many of the ostracods, especially in species of *Cypria*, *Physocypris pustulosa*, *Cypridopsis vidua*, and *Potamocypris smaragdina*. These species are commonly of varying shades of cream or light green, with blotches of dark green, brown, or black. Since these species are usually found swimming in aquatic vegetation, alga, and grass growing in the water, it is reasonable to suppose that the coloration affords them some protection from predatory animals. On the other hand,

other species of ostracods, especially species of *Candona* and *Ilyocypris*, are usually light in color, white to yellow, and are unmarked with stripes or blotches of deeper color. It may be that species such as these which live in temporary waters or creep over the bottom or through the mud in running waters are not subject to the same dangers as are species of ostracods which swim freely in the vegetation and so are apt to be eaten by plankton-consuming fishes.

#### SEASONAL DISTRIBUTION

Many of the ostracods of Illinois are seasonal in their occurrence. This is especially true of certain species which appear during the prevernal and die out in the aestival season. Other species are not found until the vernal or even the aestival season. The seasonal distribution of species collected by the writer is shown in Table 4. Since the writer has very few collections in the autumnal and none in the haemal seasons, the months from September to February inclusive are not shown in the table. Little is known of the American ostracods found during the winter months. From the fact, however, that many species are found in the prevernal season only as larvae, it is apparent that the number of species passing the winter in the adult stage is limited.

Since the seasonal distribution of the writer's collections was limited, the records of Sharpe (1897, 1908) have been taken into consideration, as indicated in the explanation to the table. By the amount of additional information given for several species by Sharpe's records, it is evident that the data on seasonal distribution are far from complete. A certain amount of valuable information, however, can be obtained from a study of the table. In the first place, it is evident that certain species are found typically in the vernal and early aestival seasons. These species include many of the *Candona*, especially those which are characteristic of temporary waters as *Candona fluviatilis*, *C. distincta*, *C. indigena*, *C. sub-urbana*, and *C. fossulensis*. Other *Candona* species are either scattered (as *C. albicans*, *C. biangulata*, and *C. punctata*) in such a way as to make the record insignificant or they are to be found during most of the year, as is *C. simpsoni* (Kofoed 1908). Of the *Cypria* species, *Cypria turneri* and *C. ophthalmica* are apparently found during the entire period from March to August inclusive. *C. maculata* shows the same distribution. *C. obesa* is evidently typical of the aestival season and later. Besides many of the species of *Candona*, *Cypricercus tuberculatus* and *C. reticulatus* appear to be forms which die out before the first of July. In addition to the *Cypria* species mentioned above, *Physocypris pustulosa* and *Cypridopsis vidua* are found throughout most of the entire period investigated. *Potamocypris smaragdina* apparently reaches its highest abundance in the

TABLE 4

Seasonal distribution as shown by the months in which each species was found. Since few collections were made in the months from September to February inclusive, these have not been shown. The name of each species is followed by the number of collections in which it occurred. The relative abundance of various species in the different months is indicated as follows: x—rare; xx—common; xxx—abundant. For the advantage of additional information, the records of Sharpe (1897, 1908) are indicated by the letter "y."

Species	Collections	Mar.	Apr.	May	June	July	Aug.
<i>Candona simpsoni</i> .....	85	xx	xyy	xxxxy	xxx	xx	x
<i>Candona punctata</i> .....	2	x	..	..	x	..	..
<i>Candona fluviatilis</i> .....	3	..	..	x	x	..	..
<i>Candona albicans</i> .....	4	..	x	..	..	xx	..
<i>Candona biangulata</i> .....	5	..	x	xy	x	..	x
<i>Candona croghaniana</i> .....	2	..	x	..	..	..	..
<i>Candona sigmoides</i> .....	4	..	..	y	x	..	x
<i>Candona caudata</i> .....	4	..	x	x	..	..	..
<i>Candona distincta</i> .....	3	..	x	x	..	..	..
<i>Candona indigena</i> .....	4	..	x	x	..	..	..
<i>Candona suburbana</i> .....	2	..	..	x	x	..	..
<i>Candona acuta</i> .....	6	..	..	xx	..	x	..
<i>Candona fossulensis</i> .....	2	..	x	..	..	..	..
<i>Cyclocypris forbesi</i> .....	1	..	y	..	..	..	x
<i>Cypria turneri</i> .....	30	xy	y	xyy	xyy	xy	xy
<i>Cypria mediana</i> .....	3	..	..	..	x	..	..
<i>Cypria obesa</i> .....	9	..	..	..	x	x	y
<i>Cypria maculata</i> .....	43	y	y	xy	xyy	xy	xy
<i>Cypria ophthalmica</i> .....	9	xy	y	xy	xy	y	xy
<i>Physocypris pustulosa</i> .....	175	..	x	xy	xxx	xyy	xyy
<i>Ilyocypris gibba</i> .....	44	..	..	xx	xxx	x	x
<i>Ilyocypris bradyi</i> .....	72	..	..	xxx	xxx	xx	x
<i>Cypricercus tuberculatus</i> .....	3	..	y	y	x	..	..
<i>Cypricercus reticulatus</i> .....	32	x	xy	xx	x	..	..
<i>Cyprinotus incongruens</i> .....	16	..	..	x	x	x	..
<i>Nolodromas monacha</i> .....	1	..	y	y	xy	y(?)	..
<i>Cypridopsis vidua</i> .....	505	xy	xy	xy	xxxxy	xxxxy	xxxxy
<i>Polamocypris smaragdina</i> .....	118	..	..	x	xxx	xx	xxxxy
<i>Darwinula stevensoni</i> .....	1	..	..	..	..	..	x
<i>Limnocythere reticulata</i> .....	70	..	y	xx	xxx	x	x
<i>Limnocythere verrucosa</i> .....	4	..	..	..	..	..	x

aestival season. The status of the two *Ilyocypris* species cannot be determined from the field data, since few collections were made by the writer from streams during March and April, and the flooded condition of streams at this time makes results untrustworthy. That the absence of these two species from the vernal collections is more apparent than real may be suggested by Sharpe's record (1908) of these two species from Colorado in March. Alm (1916) states that *I. gibba* and *I. bradyi* are found throughout the year, there being two generations. However, this does not necessarily mean that there are two generations each year in Illinois, especially since Alm states that the species in Sweden do not favor temporary waters. In Illinois, approximately one-half of the collections of these two *Ilyocypris* species were from temporary streams.

## REPRODUCTION AND ONTOGENY

No work has ever been done on the life histories and reproduction of American species except by Turner (1895) who made a study of the late larval stages of *Cypris herricki* Turner 1892, which is a synonym of *Chlamydotheca speciosa* Dana 1852 according to Furtos (1933). European writers have, on the other hand, published much on the development, reproduction, and life history of various species. Some of these studies are founded upon data secured from animals reared and observed in the laboratory (as Claus 1872); others such as the work of Alm (1916) are based largely on field collections. The writer believes either method alone to be relatively deficient and that the acceptable manner of investigation would be a preliminary study by either field or laboratory methods checked by the other method.

In general, the ontogenetic development of fresh-water ostracods is similar in different species, especially among the Cypridae. During development, nine instars occur, the last being the sexually mature animal. Claus (1872) worked out all the stages in the development of two European species: *Cypris ovum* (= *Cyclocypris ovum* (Jurine 1820)) and *Cypris fasciata* (= *Dolerocypris fasciata* (O. F. Müller 1776)). Claus found that the egg hatches into a shelled nauplius with three pairs of appendages, two representing the antennules and antennae, the third the mandibles. In general, a pair of appendages is added at each molt, with the furca appearing as two bristles in the fourth instar. Schreiber (1922) made a study of the larval stages of *Cyprinotus incongruens*. His results are slightly different from those of Claus. A comparison of the time of appearance of the appendages in the three species mentioned follows:

Instar	PAIRS OF APPENDAGES	
	<i>Cypris ovum</i> ; <i>C. fasciata</i>	<i>Cyprinotus</i> <i>incongruens</i>
1 (nauplius).....	3	3
2.....	5	4
3.....	5	5
4.....	6	5
5.....	6	6
6.....	7	7

If a single pair of appendages were added in each stage as probably occurred in the ancestors of the group, it is evident that the sixth stage would have eight rather than seven pairs of appendages. Many writers account for this irregularity by assuming that the second maxillae which are present in many crustacea have been lost in the ostracods.

Not only is there an increase in the number of appendages at many of the earlier molts, but differentiation of the appendages occurs up to the late stages. Claus (1872) found that the antennule, for instance, of the

nauplius has four podomeres, another is added in the fourth instar, one more in the sixth, and still another in the seventh. The antenna of the nauplius has two podomeres, in the sexually mature animal (ninth stage) four, and in all other stages three. The legs and furca also begin as undifferentiated structures and pass through several instars before the adult condition is reached. The second leg, for example, has one podomere when it first appears in the second stage. Three podomeres are added in the sixth instar; in the seventh stage there is an additional podomere. The anlagen of the gonads are conspicuous in the seventh instar; the copulatory organs are present in the eighth instar; and the animal reaches sexual maturity in the final stage. The development in the Cytheridae is grossly similar to that of the Cypridae (see Klie 1926a).

Not only do the appendages increase in number and change in form, but the shell becomes altered in shape in various instars. This has often led to a description of the young as a new species (see "remarks" under *Cypricercus reticulatus*). In many species, the sculpturing of the young shell differs from that of the adult, and there are differences in coloring as well. An extreme difference between young and old shells is shown in *Cypris labiata* Sars 1901 (= *Chlamydotheca incisa* (Claus 1892)) in which Sars (1901) has shown that the young shell lacks the hyaline lip-like expansion of the anterior margin as found in the adult. The young, moreover, has a row of small denticles along the posterior margin of each valve not found in the adult. Turner (1895) found much the same condition in his *Cypris herricki* already mentioned. A series of drawings by Alm (1916:pl.I) shows the shell changes in several species common in Sweden. As far as the writer knows, no work has been carried out on the early stages of even the common species in North America.

In order to complete the references regarding development, mention should be made of the work of Müller-Calé (1913) in which the early embryology through the germ layers is considered. Reference may also be given to investigations on the development of eggs and sperm, chiefly that of Woltereck (1898), Schleip (1909), and Schmalz (1912).

The manner of reproduction in ostracods varies considerably in different species. Roughly speaking, the ostracods may be divided into four groups as far as type of reproduction is concerned:

1. Males unknown; reproduction apparently always parthenogenetic:

<i>Candona fluviatilis</i>	<i>Cypricercus fuscatus</i>
<i>Candona simpsoni</i>	<i>Cyprinotus pellucidus</i>
<i>Candona biangulata</i>	<i>Cypridopsis vidua</i> *
<i>Candona caudata</i>	

\*Sharpe in 1918 considers *C. vidua* as being temporarily parthenogenetic. The present writer has seen no males, and only one record (Spandl 1925) of the occurrence of males is known. This report is questionable and has been called "unglaublich" (unbelievable) by Klie (1938a).

2. Males found in a few localities, usually absent; reproduction ordinarily parthenogenetic:

<i>Candona albicans</i>	<i>Cyprinotus incongruens</i>
<i>Ilyocypris gibba</i>	<i>Darwinula stevensoni</i>
<i>Ilyocypris bradyi</i>	

3. Males found in small numbers; reproduction supposed to be both syngamic and parthenogenetic:

<i>Cypricercus reticulatus</i>	<i>Potamocypris smaragdina</i>
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4. Males always present; reproduction thought to be syngamic:

<i>Candona punctata</i>	<i>Cypria mediana</i>
<i>Candona distincta</i>	<i>Cypria obesa</i>
<i>Candona crogmaniana</i>	<i>Cypria maculata</i>
<i>Candona sigmoides</i>	<i>Cypria ophthalmica</i>
<i>Candona recticauda</i>	<i>Physocypris pustulosa</i>
<i>Candona sharpei</i> (?)	<i>Physocypris dentifera</i>
<i>Candona indigena</i>	<i>Cypricercus tuberculatus</i>
<i>Candona suburbana</i>	<i>Notodromas monacha</i>
<i>Candona fossulensis</i>	<i>Cypriois marginata</i>
<i>Candona acuta</i>	<i>Limnocythere reticulata</i>
<i>Cyclocypris forbesi</i>	<i>Limnocythere illinoisensis</i>
<i>Cyclocypris sharpei</i>	<i>Limnocythere verrucosa</i>
<i>Cypria turneri</i>	

For details of the occurrence of males in groups two and three above, the reader is referred to the separate species descriptions given herein.

It will be noticed by reference to the last group above that a majority of Illinois species are syngamic. This group includes all the members of the family Cytheridae and many of the Cypridae. It is peculiar that many subfamilies of the Cypridae fall into more than one group as far as manner of reproduction is concerned. This variation precludes the possibility of using the manner of reproduction as a generic or specific criterion, since it is not related closely to the morphological structures used in classification.

That the method of reproduction varies in different localities is shown by Klie (1926a) regarding *Cyprinotus incongruens*. Males of this species have been found rarely in Germany and occur more frequently in Hungary and Bohemia. In North Africa, however, the males are as abundant as the females.

A definite alternation of periods of syngamic and parthenogenetic reproduction has not been shown in the ostracods. Wohlgemuth (1914) found a change from one type to another in populations under investigation in nature and in the laboratory. Whether or not an alternation similar to that in many Cladocera occurs or not is uncertain.

All the ostracods in Illinois are oviparous except *Darwinula stevensoni* which retains the eggs during development in the posterior dorsal part of the shell cavity. The eggs of oviparous species are usually attached to some substratum, especially plants, where they may undergo development at once or may remain, as in temporary ponds, for several months

surviving a period when the pond is entirely dry. The eggs are also able to withstand freezing. Because of the ability to withstand desiccation, Sars (1895, 1896, 1901) often imported mud to Norway from South America, Africa, and Australia. This mud was placed in aquaria and the ostracods allowed to develop. In this way, Sars received material not otherwise available.

The number of generations per year varies from one to many in different species. The best available example of a local species with a single generation each year is *Cypricercus reticulatus* which is chiefly an inhabitant of temporary ponds. The eggs hatch sometime during the month of March at the latitude of Central Illinois. The larval stages may be recognized by the characteristic shell reticulations which are absent in the adult. The larvae develop rapidly, and early in May the individuals become sexually mature, lay their eggs, and die. No immature individuals are ever found after the first week in May. Several other ostracod species, chiefly those living in temporary ponds, also have one generation per year. Many of these are species of *Candona* which, as a result, have a limited seasonal distribution.

On the other hand, many species have a larger number of generations. Alm (1916) often assigns a particular number of generations to a certain species, but the writer feels that his results should not be carried over without verification to the same species in North America, since there is apparently much variation under different environmental conditions. How many generations occur each year or the length of life-span are uninvestigated for American species. The present writer has observed that in *Cypridopsis vidua*, *Potamocypris smaragdina*, and probably some of the species of the subfamily Cyclocyprinae young are found nearly continuously during the summer. This would probably place these species among those with numerous generations each year.

### Food

Food and feeding in the ostracods have been given little attention by investigators. The food of few species has been studied in detail, although a study of the food habits might have some bearing on problems of distribution. In Europe, a very detailed study of the mouth parts and method of feeding in a single species has been carried out on *Notodromas monacha* by Storch (1926, 1933). Most species feed on bacteria and other minute organisms as well as detritus. Klugh (1927) in feeding experiments on *Cyprinotus incongruens*, *Cypridopsis vidua*, and *Cypria exculpta* (? — *C. turneri* sp. nov.) found that the animals ingested both algae and detritus, but in most instances thrived better when fed the former. Since the mouth parts are setaceous, they are well adapted for straining minute

organic particles from the water and forcing them into the mouth. At the same time, the mouth parts, especially the mandible, are capable of rasping material from solid bodies too large to be ingested. Many species, as some of the *Candona* species, apparently ingest large numbers of diatoms which they seem able to digest, since the cytoplasm within the test of the diatom stains when the plant is first ingested but only the empty test may be observed in the food balls in the posterior part of the intestine. In contrast to the smaller swimming species as *Cypria* spp., *Cypridopsis vidua*, and *Potamocypris smaragdina*, which feed on minute organic particles which they strain from the water, Klie (1926a) states that the larger species of Cyprinae often collect in masses to feed on the bodies of dead animals. It is probable that many of the creeping forms as *Candona* spp. and *Ilyocypris* spp. feed largely on organic materials and minute organisms in the bottom mud over which they creep.

## GEOGRAPHICAL DISTRIBUTION OF OSTRACODS

*World Distribution of Species Found in Illinois.*—The knowledge of the geographical distribution of ostracods is far from complete as a result of the lack of information relative to the faunas of many localities. In general, however, most genera and many species of ostracods are nearly cosmopolitan in their distribution. Only two well differentiated freshwater genera are known to be confined to the Western Hemisphere. The genus *Chlamydotheca*\* was said by Brehm (1939) to be the only genus restricted to the Americas. This genus is represented by an abundance of species in South and Central America and the southern part of North America. The genus *Entocythere*, species of which live in the gill cavities of crayfish, is known only from North America and was apparently overlooked by Brehm. Another genus, *Candocypris* Furtos 1933, is known only from the United States but, since it represents a transition between two well known genera (Furtos 1933), it seems inadvisable to consider it as a well defined genus as far as geographical distribution is concerned.

All the genera and many of the species of free-living ostracods found in Illinois are Holarctic in their distribution. This results in a close resemblance between European and North American ostracod faunas. While many of the species are Holarctic in their range, the species of the genera *Candona* and *Limnocythere* are often much restricted, even though the genera themselves are widespread. In the case of the *Candoninae*, this localized condition may possibly be the result of a rapid

\*Reports of species of *Chlamydotheca* from outside the Americas are based on erroneous generic determination (Klie 1930; Brehm 1932).

evolution of species occurring at the present time, as is suggested by the great specific variability and the large number of closely related species in the group. The following list indicates the geographical distribution of Illinois ostracods as determined from the literature.

1. Cosmopolitan except Australia:  
*Cyprinotus incongruens*
2. Holarctic and South America:  
*Cypridopsis vidua*                      *Cypria ophthalmica*
3. Holarctic:  
*Ilyocypris gibba*                      *Cypricercus reticulatus*  
*Ilyocypris bradyi*                      *Notodromas monacha*  
*Cypricercus fuscatus*
4. Europe and North America:  
*Candona albicans*                      *Cyprois marginata*  
*Candona caudata*                      *Darwinula stevensoni*  
*Potamocypris smaragdina*
5. North America:  
*Cypria turneri*                      *Cyprinotus pellucidus*  
*Cypria maculata* (?)                      *Physocypris pustulosa*
6. United States:  
*Cyclocypris forbesi*                      *Physocypris dentifera*  
*Cyclocypris sharpei*
7. Central United States:  
*Candona punctata*                      *Candona indigena*  
*Candona simpsoni*                      *Cypria obesa*  
*Candona distincta*                      *Cypricercus tuberculatus*  
*Candona croghaniana*
8. Illinois only:  
*Candona fluviatilis*                      *Candona fossulensis*  
*Candona biangulata*                      *Candona acuta*  
*Candona reticulata*                      *Cypria mediana*  
*Candona sharpei*                      *Limnocythere reticulata\**  
*Candona sigmoides*                      *Limnocythere illinoisensis*  
*Candona suburbana*                      *Limnocythere verrucosa*

*Distribution of Ostracods in Illinois.*—In general, the ostracods reported from Illinois may be divided into two groups: (1) those having a more or less general distribution throughout the state and (2) those limited in their distribution to restricted areas in the state. Most of the species belong to the first group. Of the species in the second group, the writer found that certain species occur only in collections from Champaign County and bordering counties, others are found only in the lakes of northeastern Illinois, and still others are confined to the southern portion of the state where the waters are often acid. The localized occurrence of certain species in Champaign County is not particularly significant

\*As explained in "remarks" under the description of this species, the record of *L. reticulata* for Maine appears to be erroneous as a specific determination. Therefore, *L. reticulata* is included with the species limited to Illinois rather than with those from the United States.

since the writer made an intensive study of the vernal ponds in the region and, as a result, found species which probably escaped collection in other parts of the state. Of considerable significance, however, is the restriction of certain species to the Chicago region and to the southern portion of the state. Among the ostracod species apparently found only in the Chicago region may be listed *Cypricercus tuberculatus*, *Notodromas monacha*, *Cyprois marginata*, *Darwinula stevensoni*, and *Limnocythere verrucosa*. Three of these, *Cypricercus tuberculatus*, *Darwinula stevensoni*, and *Limnocythere verrucosa* are found only in the lakes of glacial origin northwest of Chicago. Two species, *Candona punctata* and *Cypria mediana*, appear to be confined to the southern part of the state.

## MORPHOLOGY OF FRESH-WATER OSTRACODS

For a complete understanding of the relationships among groups and species of the Ostracoda and in the use of the diagnostic keys, a working knowledge of morphology is necessary. The descriptive morphology as given here is offered not as a complete treatise on the subject but as an aid in systematic work.

### SHELL

The body of the fresh-water ostracod is completely enclosed by a bivalve shell (fig. 96) from which no part of the body extends when the shell is entirely closed. When the animal is active, however, the appendages used in swimming and creeping extend ventrally and anteriorly from between the laterally placed valves (fig. 1). These valves are duplicatures of the skin folds continuous dorsally with the body of the animal. Each skin fold secretes shell material from both its surfaces, and the outer and inner plates thus formed are fused together along the anterior, posterior, and ventral margins of the shell. The outer plate is often more or less calcified throughout its extent, but the calcified area of the inner plate is limited to the marginal portion of the valve. The valves are often unequal (figs. 96, 121), as either valve may overlap the other along certain portions of the margin when the shell is closed. The nature of the overlap is usually a useful specific characteristic. Anterior, ventral, posterior, and dorsal margins are recognized. In some species of ostracods, the margin of the valve along a part or all of its length may display tubercles (figs. 116, 128), crenulations, or other structural markings. Often a hyaline border extends beyond the margin and may form an extensive lip (fig. 118). Pore-canals (fig. 128-P) occur in many species as minute canals lying between a submarginal line and the margin. When the submarginal line and the margin are far separated, the pore-canals are long and con-

spicuous; when, however, the margin is approximate to the submarginal line, the pore-canals may become obliterated.

The shell halves are connected along the dorsal margin by an elastic band sometimes reinforced in the Cytheridae by a toothed, locking structure (fig. 137-AT, PT) which makes the closing of the valves more certain. The halves are unconnected along the anterior, posterior, ventral, and the fore- and hind-dorsal margins. The elastic hinge opens the shell much after the manner in which opening of the shell is carried out in bivalve molluscs. The closing of the shell is brought about by the contraction of a bundle of adductor muscles which extends from one valve to the other, passing transversely through the body of the animal. The area of attachment (figs. 40-M, 127-S) of the adductor muscles is conspicuous on the valves of the shell. These muscle scars are located anterior to the middle of each valve.

The nature of the surface of the valves often provides specific characters useful in diagnosis. Variations occur in both surface sculpturing and color. The shell surface may be smooth, pitted, or papillose. Setae are commonly present along the valve margins and to a varying degree on the shell surfaces. These setae may arise in connection with surface sculpturing (fig. 103) or may occur independently of such markings (fig. 118). In many instances, the color of the valve surface is so characteristic that the species may be determined by skillful examination of the color even in preserved material. In examining the shell for color, both reflected and transmitted light should be used in order to detect faint markings to the best advantage. In some instances, weak or faded markings are revealed only after the shell has been cleared in glycerine. Brown, green, or whitish gray are the prevailing colors. Color bands or blotches are usually of a darker shade of green, brown, or black. Some species exhibit a mother-of-pearl sheen when the valves are dried.

The size of the shell varies considerably in different species. The minimum length of the mature shell in any species is about 0.25 mm. while the maximum length of the shell is 21.0 mm. in a marine species of the genus *Gigantocypris* (G. W. Müller 1912). Fresh-water forms seldom exceed 3.0 mm. in shell length and in most cases are under 1.0 mm.

#### BODY SEGMENTATION AND APPENDAGES

The shortened body of an ostracod shows externally no trace of segmentation except as indicated by the metamerically arranged appendages (fig. 1). The boundary between the two body parts, the head and thorax, however, is marked by a slight constriction; the abdomen is wanting. The cephalic region bears four pairs of appendages: the antennules, the antennae, the mandibles, and the maxillae. The thoracic

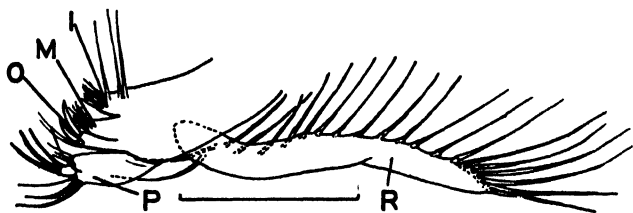
region has three pairs of appendages: the first, second, and third thoracic legs. The body ends in a pair of furcal rami (except in *Darwinulidae*) homologous to the post-abdomen of the *Cladocera*. In the fresh-water species, the appendages, including the antennae, are formed chiefly of the endopodite as a result of the loss or reduction of the exopodite.

The two or three eyes (fig. 1-E), which are separated in the primitive condition, are fused together to varying degrees. The eyes are usually located in the dorsal part of the head anterior to the shell hinge and are mounted on a low dorsal projection near the base of the antennules. The eyes appear as a dorsal colored fleck when the shell is gaped. When the shell is closed, the eyes may be seen as a pigment spot through the shell in species having translucent valve lamellae. The eyes and the upper and lower lips are not often mentioned in taxonomic work.

Anterior and dorsal to the mouth may be found the first cephalic appendages, the antennules (fig. 1-AU) (often referred to as the first antennae). The antennules are uniramous, the exopodite being lost. Typically each antennule is composed of eight podomeres but through fusion may approach a condition in which there are only five. The basal portion or protopodite consists regularly of two podomeres which some writers believe to be a single divided podomere (cf. Furtos 1933; Klie 1938a). In the *Cypridae*, the endopodite consists typically of five podomeres; in the fresh-water *Cytheridae* of North America it is reduced to three or four podomeres. The antennules usually carry short, stiff, claw-like bristles for digging and climbing (*Darwinulidae* and *Cytheridae*) or long, feathered setae for swimming (fig. 1-N) (majority of the *Cypridae*).

The second pair of cephalic appendages are the antennae (fig. 1-AN). These are termed the second antennae when the antennules are designated as the first antennae. Each antenna includes a protopodite of one or two podomeres and an endopodite of three or four podomeres. The exopodite is reduced to a scale usually bearing three setae in the *Cypridae*, to a long bent seta (fig. 131-F) containing the duct of a gland secreting adhesive material in the *Cytheridae*, or is entirely vestigial in the *Darwinulidae*. On the posterior margin of the first podomere of the endopodite in the *Cypridae* is found a sensory organ (figs. 8-S, 106-O). This same podomere often carries close to its distal end a group of five long setae (fig. 1-V) which, when well developed, are used in swimming by many of the *Cypridae*. These setae are greatly reduced in the *Cytheridae* and the *Darwinulidae*, and are wanting in the *Candoninae* of the *Cypridae*. Claws are found on the ultimate podomere of the endopodite. The antennae function in locomotion, in feeding, as a sensory structure, and in the male as an organ for holding the female during copulation.

The third pair of cephalic appendages are the mandibles located at the sides of the mouth. Each mandible (figs. 1-M, 43) consists of a base of two podomeres, a palp which represents the endopodite, and a branchial plate (fig. 43-R) (sometimes reduced to a few setae) which is modified from the exopodite. The basal portion is highly chitinized as it is to this portion that the muscles used in operation of the mandibles are attached. The distal end of the mandible is truncate and provided with strongly chitinized teeth (fig. 43-C). The palp (fig. 1-P) consists of the three podomeres of the endopodite and the second podomere of the base. It bears claws and setae.



TEXT-FIGURE.—Mesial view of the left maxilla of *Candona acuta* sp. nov. (female). I—inner masticatory process; M—middle masticatory process; O—outer masticatory process; P—palp; R—respiratory plate. Scale: 0.2 mm.

The fourth pair of cephalic appendages are the maxillae, as shown in the accompanying text-figure. These are the first maxillae of many of the older authors, since this pair of structures is homologous with the first maxillae of other crustaceans. The base of the maxilla has typically three narrow distal masticatory processes and a palp of two or three podomeres. The exopodite is well developed, forming a branchial plate. The shape and number of setae on the masticatory process closest to the palp are of considerable taxonomic importance. This process has been variously called *the* masticatory process, the third masticatory process, and the outer masticatory process. The last is preferred by the present writer. In some Cytheridae, the palp and processes may be reduced.

The mandibles and the maxillae are the feeding structures, but the first thoracic leg sometimes assumes a similar structure and function. The mandibles not only break food into small particles but the palp helps in sweeping food toward the mouth. The mandibles are supported in function by the maxillae whose processes push food toward the mouth, while the branchial or respiratory plate not only removes excess and inappropriate food but also by its vibration creates a current of water for use in respiration. In reference to the masticatory processes, both the English term and its German equivalent (Kauladen) are misnomers, as the processes do not chew the food but merely pass particles toward the

mouth. The second maxillae are wanting in the Ostracoda, but in the older literature the term is sometimes applied to the first thoracic legs.

The thoracic portion of the body bears three pairs of appendages (figs. 1-R, L, T) except in the males of the Cytheridae, which have a pair of sensory structures (fig. 135) considered by some writers to be a fourth pair of thoracic appendages. The nature of the legs is a useful criterion for division of the fresh-water Podocopa into families. In the Cytheridae the first, second, and third pairs of legs are similar in structure and are pediform; in the Darwinulidae, only the second and third pairs are similar; and in the Cypridae, all the legs differ in structure.

The first thoracic leg (fig. 1-R) is often highly modified, and in the Cypridae so resembles the maxilla that it is designated in the older literature as the second maxilla. The first leg has at times also been referred to as the maxillary foot or maxilliped because of its resemblance to a "chewing foot" or jaw. In the Cypridae, the basal podomere or protopodite ends in a masticatory process bearing setae (fig. 9). The endopodite is modified as a palp often of a single podomere and the exopodite forms a branchial plate which may be reduced to one or a few setae as in the Cypridopsinae and Candoninae (fig. 9-R). The palp in the male is often modified to form a prehensile claw (figs. 22, 71) of one or two podomeres for use during copulation. When the prehensile palp is formed of two podomeres, the proximal one is called the propodus (fig. 122-P); the distal one is termed the dactylus (fig. 122-D). The first leg in the Cytheridae is similar to the other two thoracic legs, since it consists of an anteriorly directed protopodite carrying a pediform endopodite of three or four podomeres. The exopodite or branchial plate is wanting. In the Darwinulidae, the structure of the first leg is midway between the condition found in the other two families, since the masticatory process as well as the branchial plate is well developed, as in many Cypridae, and the endopodite is a pediform structure of three podomeres similar to that of the Cytheridae.

The second thoracic legs (fig. 1-L) (first thoracic legs according to those authors who recognize the here-designated first thoracic legs as second maxillae or maxillipeds) are uniramous and consist of a protopodite and a backwardly directed pediform endopodite at the end of which is usually a more or less curved claw (fig. 26-C). The endopodite consists usually of three or four podomeres, but in some species it may appear to have an additional podomere through a division of the next to the last podomere. The exopodite is lacking.

The third thoracic legs (fig. 1-T) (designated as second thoracic legs by those authors who describe the first pair of legs as second maxillae or maxillipeds) usually consist of five podomeres. The third leg is similar

to the second in the Cytheridae and the Darwinulidae, but in the Cypridae it consists of a basal podomere and an endopodite typically of three podomeres (fig. 4), of which one may be divided (fig. 53-P). In the Cypridae, this leg is modified as a cleaning foot (German: "Putzfuss") by being bent dorsally and by being distally adapted for use in keeping the shell and body free of foreign material. The modification consists either of the presence of several unequal setae, usually three in number and often reflexed in position, or a complicated pincer apparatus or chela formed from the last two podomeres of the third leg (fig. 120) in the Cyprinae *s. str.*

A possible fourth pair of thoracic appendages may be found in the so-called "brush-like" organ (German: "bürstenförmige Organ") (fig. 135) in the males of the Cytheridae. This appendage carries a tuft of setae and is richly supplied with nerves. Its structure has led to the assumption that it is a sexual sensory organ.

At the posterior end of the body in the Cypridae and the Cytheridae there are paired appendages which are the remains of the abdomen. When at rest, these furcal rami are directed ventrally between the third legs. By being articulated with the body, they are capable of movement and assist in locomotion. Typically, each appendage (fig. 69) consists of a basal portion or ramus proximally articulated with the body and ending distally in two setae and two claws. Various modifications may occur in the Cypridae by the loss or reduction of one or more of the claws or setae. The extreme degree of reduction in the Cypridae occurs in the Cypridopsinae where each furcal ramus is reduced to a small base, a dorsal seta, and a whip-like terminal part often referred to as the "flagellum" (fig. 117). In the Cytheridae, the furcal rami are very much reduced (figs. 132, 138); in the Darwinulidae, they are entirely wanting and the thorax ends in a short cone-shaped process (fig. 126).

#### RESPIRATORY, CIRCULATORY, EXCRETORY, DIGESTIVE, AND NERVOUS SYSTEMS

Respiration in the fresh-water ostracods is accomplished by gaseous exchange through the entire surface of the body and especially through the membranous inner lamella of the shell. Bernecker (1909) found the inner shell lamella in *Cyprinotus incongruens* to be made up of seven large respiratory cells which form a respiratory epithelium overlying the valve cavity which constitutes a blood sinus. The renewal of water within the shell cavity is accomplished by the movements of the appendages. Thus the respiratory plates of some of the appendages not only provide additional respiratory surface but also bring oxygenated water into contact with other body surfaces.

Like the gills, the heart is also wanting in fresh-water ostracods, although some marine species have a pulsating sac (Klie, 1926a). Whether or not there is any adaptation for circulating the body fluids in forms lacking a heart is not known.

The excretory system in several species of European ostracods is described in detail by Bergold (1910). There are three excretory organs: the glands of the antennules, the shell glands, and the maxillary glands. Each of the glands of the antennules is small and opens to the outside ventral to the base of each antennule. The shell glands lie in the anterior part of the shell between the lamellae, and their ducts lead to the outside in the region of the second antennae. The third pair of glands are the maxillary glands. Each of these consists of a coelomic sac and a urinary duct, and one lies in the body at the base of each maxilla. By muscular constriction, the excretion is forced from the sac into the looped canal or duct.

Both Claus (1895) and Bergold (1910) discuss in detail the digestive system. The alimentary canal consists of three parts: the esophagus or fore-gut, the mid-gut, and the hind-gut. The food material in the form of minute organic particles is collected together in the atrium bounded by the mouth parts. Here the particles are cemented together by secretions from glands in the upper lip and in the base of the mandible near the distal teeth. This food is passed down the esophagus into the anterior portion of the mid-gut where the cells lining the tract are secretory and also function in absorption of nutritive material. The largest digestive gland is the paired hepato-pancreas or so-called liver which lies between the shell lamellae and empties into the mid-gut. The straight and short end-gut leads from the mid-gut to the anus which is located behind the furca. Food balls may be seen in the mid-gut when the animal is examined by transmitted light.

Good accounts of the nervous system in certain species of Cypridae are given by Turner (1896) and Hanström (1924). The nervous system in the fresh-water Cytheridae seems to have received no attention. In general "the central nervous system consists of a supra-oesophageal ganglion which is united to a ventral chain by a pharyngeal collar" (Turner 1896). The supra-esophageal ganglion is made up of a large number of fused ganglia, probably as many as seven (Turner 1896). The anterior group of fused ganglia of the ventral chain is usually designated as the infra-esophageal ganglion (Klie 1926a) and is made up of at least three ganglia. The antennules and the antennae are innervated by the supra-esophageal ganglion which is also connected to the optic ganglion of the eye. The infra-esophageal ganglionic mass innervates the mouth parts and the closing muscle of the shell. Posterior to the infra-esophageal mass, there lie the two paired ganglia of the ventral chain. The first

innervates the first thoracic legs, the second gives off paired nerves to the second and third thoracic legs and an unpaired nerve to the sexual apparatus. While the ventral ganglia in the species examined by Turner (1896) are well separated, Hanström (1924) found the infra-esophageal ganglion and the visceral ganglia of the ventral chain to be fused closely together in certain European species of Cypridae.

The sensory organs include the eye, tactile receptors, and chemoreceptors. The eye usually consists of three optic systems more or less fused together and is placed dorsal to the base of the antennules. The eye is made up usually of three pigment cups, one median and two lateral (Nowikoff 1908). Nowikoff, in working chiefly on European species of the subfamily Cyprinae, found that each eye cup contains a number of eye cells forming a concave retina. The number of cells in each lateral cup is ten to fifteen, in the median one only seven or eight. The tactile organs are in the form of setae scattered over the shell and body. There are also well developed specialized tactile setae on many of the cephalic appendages.

One very important sensory organ (fig. 8-S) is the one on the antepenultimate podomere or first podomere of the endopodite of the antennae in the Cypridae. This has been considered an olfactory organ.

#### REPRODUCTIVE SYSTEM

The female sexual organs consist of paired ovaries, oviducts, seminal receptacles, and genital openings. In the Cypridae the ovaries lie in the space between the lamellae of each valve (figs. 18-O, 40-O) where in many species they may be seen by transmitted light. In the Cytheridae the ovaries lie lateral to the mid-gut in the body of the animal. Each oviduct is joined near the outer end by the duct from the seminal receptacle. The female genital openings lie between the third thoracic legs and the furcal rami and may be at the end of distinctly well developed paired genital lobes (figs. 30-G, 37-G) as in many of the Candoninae.

In the Cypridae, the testes lie in the cavity of the valves (figs. 21-T, 41-T), and each testis usually consists of four branches. The branches unite to form the vas deferens of each side as they leave the valve cavity dorsal to the muscle scars. The vas deferens makes several coils or loops and then enters the dorsally and posteriorly located ductus ejaculatorius or Zenker's organ (figs. 93, 123) which by alternate contraction and expansion forces the sperms into the penis during copulation. The paired copulatory organs are located posteriorly to the ejaculatory ducts and serve to carry the sperm to the female. Each copulatory organ or penis often has three lobes but some of these may be wanting (figs. 57, 72, 81).

Like the ovaries, the testes in the Cytheridae lie along the intestine in the body proper. In members of this family there is no ductus ejacu-

latorius. The copulatory organ consists of paired plates often with several appendages (figs. 134, 141).

## TAXONOMY

### ORDER OSTRACODA

The Ostracoda, for which the common name "mussel-shrimps" (German: "Muschelkrebse") has been suggested by Johansen (1921), include those crustacea which are enclosed by a dorsally hinged bivalve shell and which never have more than four pairs of postoral appendages. The ostracod shell bears some resemblance to the shells of certain Phyllopoda (Conchostraca) but may be readily distinguished from the phyllopod shell by the lack of growth lines. Furthermore, the Ostracoda may be easily and certainly separated from the shelled Phyllopoda by the specialized appendages of the former in contrast to the large number (at least twenty) of foliaceous postoral appendages in the latter. On superficial examination the shell of certain of the small bivalve molluscs (as the Sphaeriidae) may also be mistaken for an ostracod shell by one not familiar with the gross appearance of the forms. These may be readily differentiated from ostracods by the presence of growth lines on the shell and the lack of jointed appendages.

The order Ostracoda (with reference only to recent species) contains about fifteen hundred valid species and perhaps nearly a thousand additional species of uncertain status. Many ostracods are marine but there are approximately five hundred recognized species from fresh waters.

### SUBORDERS OF THE ORDER OSTRACODA

The order Ostracoda may be divided into four suborders, based chiefly on the nature of the shell, the number of postoral appendages, and the character of the furca. The Ostracoda of fresh waters belong entirely to the suborder Podocopa *s. str.*, which also includes some marine species. The other three suborders are strictly marine.

The suborder Podocopa *s. str.* may be characterized as follows: Shell without a permanent aperture anteriorly. The antenna with the endopodite well developed, but the exopodite, at the most, represented by a single long seta (fig. 131-F) or small setae-bearing scale. Both antennules and antennae are used in locomotion, either in swimming or creeping. The mandibular palp consists of four podomeres (figs. 25, 43). The heart is wanting; eyes are usually present. Four pairs of postoral appendages are present. Caudal ramus, when well developed, rod-shaped (fig. 37-B); often reduced (figs. 117, 132). Inhabitants of fresh and marine waters. Over one-half of the known ostracods belong to this suborder.

For completeness and general information, some indication of the characteristics of the three strictly marine suborders and a comparison of their structure with the suborder Podocopa is given here:

(a) The suborder Myodocopa *s. str.* is characterized by having at the anterior end of the shell a permanent opening through which the antennae may be extended for use in locomotion when the shell is otherwise tightly closed. The antennules are not highly developed for swimming. There are four pairs of postoral appendages, and the furca is lamelliform. A heart is present. The suborder Podocopa *s. str.* may be separated from the suborder Myodocopa *s. str.* by a lack of a permanent anterior shell opening, the absence of a heart, and the presence of a bar-like rather than a lamelliform furca.

(b) The suborder Cladocopa may be separated from the suborder Podocopa *s. str.* by the presence in the former of only two pairs of postoral appendages and by having the body terminate in reflexed lamelliform processes bearing numerous spines. The heart and eyes are absent in the suborder Cladocopa.

(c) The suborder Platycopa is characterized by biramous antennae, both branches being well developed with broad flattened podomeres. There are three pairs of postoral appendages, none of them distinctly leg-like. The furcal ramus is leaf-like, widened distally, and the margin bears many spines. The eye and heart are wanting. The subfamily Podocopa *s. str.* may be separated from the Platycopa by the presence in the former of four pairs of postoral appendages, usually well developed eyes, poorly developed exopodite of the antenna, and the bar-like furcal ramus.

While Sars (1928) and Klie (1938a) follow the division of the order Ostracoda into four suborders as given herein, G. W. Müller (1912, 1927) follows a different scheme and divides the order Ostracoda into two suborders: Myodocopa and Podocopa. The first suborder embodies the Myodocopa *s. str.* and Cladocopa as used herein; and the second combines the Platycopa and the Podocopa *s. str.* as recognized by the present writer. The system in which the order Ostracoda is divided into two suborders rather than four is certainly not a natural classification and is therefore to be avoided. Skogsberg (1920) recognizes five suborders, the additional group being formed by a division of the Myodocopa. Since the Myodocopa are entirely marine, no discussion need be given here of Skogsberg's classification.

#### FAMILIES OF THE SUBORDER PODOCOPA *s. str.*

The suborder Podocopa *s. str.* includes four families, three of which are found in fresh waters. If the suborder Podocopa is considered in the broad sense (as by G. W. Müller, 1912, 1927), then a fifth family, the family Cytherellidae, must be added to include the single marine genus

*Cytherella*. *Cytherella*, however, has many characteristics which are above the rank of family criteria and so is properly placed by itself in the suborder *Platycopa*.

The four families recognized herein as belonging to the suborder *Podocopa s. str.* are the families *Cypridae*, *Darwinulidae*, *Cytheridae*, and *Nesideidae*.\* Of these, the family *Nesideidae* is strictly marine, *Darwinulidae* is entirely fresh-water, *Cytheridae* is chiefly marine with a few fresh-water genera, and *Cypridae* is common in both marine and fresh water. The following tabulation shows the chief structural differences among the four families of the suborder *Podocopa s. str.*

Family	Teeth of shell hinge	Exopodite of antenna	Thoracic legs	Furcal ramus
<i>Cypridae</i> .....	None	Reduced to a small scale bearing setae	All different	Usually well developed
<i>Darwinulidae</i> .....	None	Greatly reduced	Second and third similar	Wanting
<i>Cytheridae</i> .....	Present or vestigial	Large seta forming a gland duct	All similar	Reduced
<i>Nesideidae</i> .....	None	Small scale bearing a few setae	All similar	Well developed

#### KEY TO FAMILIES OF THE SUBORDER PODOCOPA IN ILLINOIS

- 1a. Exopodite of the antenna in the form of a long hollow seta carrying the secretion from a gland near the base of the antenna (fig. 131-F); the thoracic legs similar.....Family *CYTHERIDAE*
- b. Exopodite of the antenna not as in the family *Cytheridae*; the thoracic legs not all similar.....2
- 2a. Second and third thoracic legs similar in structure and direction; furca wanting.....Family *DARWINULIDAE*
- b. Second and third thoracic legs differ in structure and the direction of extension (fig. 1-L, T); furca present but sometimes much reduced.....Family *CYPRIDAE*

#### FAMILY CYPRIDAE

Surface of the shell usually smooth; dorsal margin without interlocking teeth. Eyes developed to varying degrees; either separated or fused into a single median eye. The antennules with a basal portion of two or three podomeres and an endopodite of four or five podomeres, with swimming setae well developed. The antenna with a basal part of

\*The family *Nesideidae* should perhaps be replaced by *Bairdiidae* since the two names appear to be synonyms, at least by virtue of their having synonymous type genera, *Bairdia* M'Coy 1844 being recognized as synonymous with *Nesidea* Costa 1847. The genus *Bairdia* and the family *Bairdiidae* have long been accepted by geologists in reference to fossils. The genus *Nesidea* and the family *Nesideidae* have, on the other hand, been used extensively by zoologists working on recent material. Sars (1928) approves the use of *Bairdia* rather than *Nesidea* for recent species and this practice should perhaps be followed.

two podomeres and an endopodite of three or four podomeres. The exopodite is reduced to a small scale-like appendage bearing at the most three setae. First thoracic leg not pediform but modified as a mouth part, with the anterior margin of the base adapted for feeding. The endopodite of the first leg forms a small palp in the female but is enlarged to form prehensile organs in the male (figs. 63, 122). The second thoracic leg has an endopodite of three or four podomeres and a strong distal claw (fig. 26). The third leg is bent dorsally and is probably used in cleaning the respiratory surfaces and other parts of the body. The third leg usually has three distal setae (fig. 27) but the distal end may be modified for grasping (fig. 120). The furca is typically well developed and rod-shaped (fig. 11) but may be reduced to a "flagellum" or whip-like structure (fig. 117) (Cypridopsinae). The gonads are located within the valves of the shell. In the male, a portion of the vas deferens is modified to form an ejaculatory duct (fig. 93). The family Cypridae is large and includes the majority of fresh-water ostracods.

Since the family Cypridae is so large, it has been convenient to subdivide it into several subfamilies. Two well recognized subfamilies, Pontocyprinae and Macrocyprinae, are strictly marine and merit no further consideration here. Fresh-water representatives of this family have been systematized into a varying number of subfamilies. G. W. Müller (1912, 1927) recognizes, in addition to the two marine subfamilies mentioned, only three subfamilies in the Cypridae; the subfamily Candoninae (Candocyprinae of some authors), the subfamily Ilyocyprinae, and the subfamily Cyprinae. Two of these subfamilies are conglomerations of genera with greatly diversified characterization and as a result the groupings are distinctly unnatural. In order to form natural groupings, as far as the subfamilies are concerned, it is necessary to split the Candoninae and the Cyprinae into smaller groups, each representing a single genus or a group of closely related genera. Kaufmann as early as 1900 (1900b) divided the family Cypridae into eight subfamilies. His system is usable with a few minor corrections in orthography and a combination of his subfamilies Herpetocypridinae and Cypridinae into the subfamily Cyprinae *s. str.* The fresh-water subfamilies of the family Cypridae may be listed as follows, with the two recognized schemes in parallel columns:

<i>Subfamilies according to G. W. Müller (1912, 1927) and Klie (1938a)</i>	<i>Subfamilies after Kaufmann (1900b); used by Wagler (1937) and the present writer</i>
Candoninae (Candocyprinae).....	{ Candoninae <i>s. str.</i> Cyclocyprinae
Ilyocyprinae.....	Ilyocyprinae
Cyprinae.....	{ Cyprinae <i>s. str.</i> Cypridopsinae Notodrominae

All the subfamilies listed to the right are strictly fresh-water inhabitants except the subfamily Cyclocyprinae which has, in addition to several genera found in fresh water, a single genus which is marine.

# KEY TO SUBFAMILIES OF THE FAMILY CYPRIDAE FOUND IN FRESH WATERS

- 1a. Furcal rami greatly reduced, whip-shaped, without a terminal claw at the end (difficult to observe) (fig. 117).....Subfamily CYPRIDOPSINAE
- b. Furcal ramus well developed, bar-shaped, with two terminal or subterminal claws (fig. 11).....2
- 2a. Outer masticatory process of the maxilla with six nearly equal setae modified to form toothed spines (fig. 113).....Subfamily NOTODROMINAE
- b. Outer masticatory process with two or three of the setae modified as spines...3
- 3a. Swimming setae of the antenna completely wanting (fig. 8).....Subfamily CANDONINAE *s. str.*
- b. Swimming setae of the antenna present (fig. 1-AN, V).....4
- 4a. Third thoracic leg distally modified as a seizing apparatus, the ultimate podomere being beak-like with two well developed bristle-like setae, the third seta wanting or hook-like (fig. 120).....Subfamily CYPRINAE *s. str.*
- b. Third thoracic leg not bearing a chela, last podomere cylindrical and bearing three setae (figs. 53, 75).....5
- 5a. Shell elliptical to subrectangular (fig. 99), swimming setae of the antenna do not extend much beyond the tips of the end claws; palp (endopodite) of the first thoracic leg small, pediform, of two or three podomeres.....Subfamily ILYOCYPRINAE
- b. Shell usually short and rounded (fig. 73), at least not subrectangular; swimming setae of the antenna extend well beyond the terminal claws (in Illinois species); the palp of the first thoracic leg of one or two podomeres in the female, always two in the male; not pediform..Subfamily CYCLOCYPRINAE

## SUBFAMILY CANDONINAE *s. str.*

Shell white, porcelain-like, often with mother-of-pearl sheen when dry. Swimming setae of the antennae absent (fig. 8). Two special sensory setae are usually located at the juncture of the fourth and fifth podomeres of the male antenna. Respiratory plate (exopodite) of the first thoracic leg with two or three setae (fig. 9-R); palp (endopodite) in male and female unjointed. Third thoracic leg with three unequally long setae on the last podomere (fig. 4), the penultimate (third) podomere either divided (fig. 53-P) or undivided (fig. 10-P). If divided, the third leg has five apparent podomeres. Ejaculatory apparatus of the male usually with seven wreaths of chitinous spines; openings of the ejaculatory duct funnel-shaped.

The Candoninae are creeping and burrowing forms as indicated by the lack of swimming setae on the antennae. The members of this group

are found in a variety of habitats and are widely distributed. Many species, however, are taken sparsely because they are often limited seasonally and do not occur in great abundance.

The subfamily Candoninae contains, according to some authors, as many as five genera. Of these five genera, two, *Candona* and *Paracandona*, are found in North America. The genus *Candona* alone has been found in Illinois. Almost without exception, the Candoninae are restricted to the Holarctic Region.

#### GENUS CANDONA BAIRD 1845

Valves of the shell white, sometimes transparent; may have a mother-of-pearl sheen; surface smooth, sometimes with scattered puncta and hairs; hairy in some species. Shell variable in shape and size, elongated ovoid to reniform (fig. 50), sometimes with a straightened dorsal margin and truncated ends (fig. 65). Swimming setae of the antennae absent (fig. 8); the antennae of five podomeres in the female, often of six apparent podomeres in the male through a division of the penultimate; two male setae often present at the juncture of the two divisions. The last two podomeres of the mandibular palp short, rounded (fig. 43). Respiratory plate of the first thoracic leg rudimentary, usually with two unequal setae, never more than three (fig. 9-R). The third thoracic leg commonly of four podomeres; sometimes appearing to consist of five podomeres through a division of the third or penultimate podomere (fig. 53-P). When such a division occurs, there is no seta at the juncture of the two divisions. The terminal podomere of the third thoracic leg is short and bears two backwardly directed setae (fig. 4-C) and one long forwardly directed seta. The furcal ramus (fig. 11) is strong, bearing two strong claws and one or two setae; the dorsal seta often being removed from the subterminal claw by about twice the least width of the ramus. Male sexual organs with the characteristics of the subfamily.

Fifteen species of the genus *Candona* have been found in Illinois. Of these, six are described herein as new species. Of the six species of *Candona* reported for Illinois by Sharpe (1897), the present writer has rediscovered and added to the description of two, has redescribed one as a new species on the basis of additional material which showed that it is not the European species to which it was assigned by Sharpe, and has found one to be a synonym. Two of Sharpe's reported species were not found in the present writer's collections. One of these two, however, was assigned a new name because the individuals as described obviously do not belong to the species to which they were assigned by Sharpe.

The genus *Candona* is a very large one, over one hundred and fifty

species being reported in the literature. A lack of understanding of the relationships among species has resulted in the genus as a group becoming taxonomically unwieldy. Following a failure to divide the genus *Candona* by placing some of the species in new genera, various attempts have been made to divide the genus into groups. The groups suggested are of less than sub-generic value and each group is based on a type species. As early as 1900, G. W. Müller divided the genus as found in Germany into three groups. A discussion of this and later groupings may be found in Furtos (1933). The present writer has followed the system given by Klie (1938a) who has greatly modified the earlier scheme. According to Klie, there are seven groups in the genus *Candona*: groups *Candida*, *Rostrata*, *Fabaeformis*, *Compressa*, *Acuminata*, *Cryptocandona*, and *Mixta*. A key to these groups based on the work of Klie is given herewith.

#### KEY TO GROUPS OF THE GENUS CANDONA

- 1a. The branchial plate of the first thoracic appendage has two setae (fig. 9-R)...2
- b. The branchial plate has three setae.....6
- 2a. The medial seta on the distal margin of the next to the last podomere of the mandibular palp feathered.....Group CANDIDA
- b. The above-mentioned seta unfeathered.....3
- 3a. Sexual lobe of the female mostly rounded (fig. 11-G); when pointed, then short and not prolonged lappet-like toward the posterior (fig. 15-G). Shell rounded; typically but not necessarily, the height is greater than one-half the length (fig. 2).....4
- b. Sexual lobe of the female pointed and prolonged lappet-like toward the posterior (fig. 69-G). Shell typically elongated, height usually but not always less than one-half the length (fig. 58).....5
- 4a. Three setae in the bundle on the inner margin of the antepenultimate podomere of the mandibular palp.....Group ROSTRATA
- b. More than three setae in the bundle (fig. 25-B).....Group COMPRESSA
- 5a. Either three or five setae in the bundle on the inner margin of the antepenultimate podomere of the mandibular palp.....Group FABAEFORMIS
- b. Four setae in the bundle (fig. 43-S).....Group ACUMINATA
- 6a. A seta is present in the middle of the penultimate podomere of the third thoracic leg.....Group CRYPTOCANDONA
- b. The mentioned seta lacking.....Group MIXTA

All seven groups of the *Candona* may be found in North America with the exception of the groups *Cryptocandona* and *Mixta*. It is impossible, because specific descriptions are incomplete, to assign some of the American forms definitely to the proper group. Moreover, there is some confusion in regard to many American forms because, as the groups are built around European type-species, American species do not always fit perfectly into this apparently artificial scheme.

The possible group assignments of species occurring in Illinois are as follows:

## Group Rostrata

- C. simpsoni* Sharpe 1897  
*C. punctata* Furtos 1933  
*C. fluvialis* sp. nov.

## Group Compressa

- C. albicans* Brady 1864  
*C. biangulata* sp. nov.

## Group Fabaeformis

- C. sharpei* sp. nov. (very questionable assignment)

## Group Acuminata

- C. crogmaniana* Turner 1894  
*C. sigmoides* Sharpe 1897  
*C. recticauda* Sharpe 1897  
 (probable assignment)  
*C. sharpei* sp. nov.  
 (questionable assignment)  
*C. caudata* Kaufmann 1900  
*C. distincta* Furtos 1933  
*C. indigena* sp. nov.  
*C. suburbana* sp. nov.  
*C. acuta* sp. nov.  
*C. fossulensis* sp. nov.

## KEY TO SPECIES OF THE GENUS CANDONA IN ILLINOIS

(Based on characters available in the female)

- 1a. Penultimate podomere of the third thoracic leg undivided (fig. 10-P).....2
- b. Penultimate podomere of the third thoracic leg divided (leg of five apparent podomeres) (fig. 53-P).....4
- 2a. Shell with high rounded arch dorsally; height more than one-half the length (fig. 2).....*C. punctata* Furtos 1933
- b. Shell lacking a high rounded arch dorsally; height equal to or slightly less than one-half the length.....3
- 3a. Dorsal margin of the shell flattened and horizontal (fig. 6).....*C. fluvialis* sp. nov.
- b. Dorsal margin of shell forms a low evenly rounded arch (fig. 12).....*C. simpsoni* Sharpe 1897
- 4a. Shell of female less than 0.90 mm. in length.....5
- b. Shell greater than 0.90 mm. in length.....6
- 5a. Shell with a conspicuous dorsal-anterior sinuation; anterior end narrowly rounded (fig. 24). Genital lobe of female conspicuous but small, cone-shaped (fig. 28-G).....*C. biangulata* sp. nov.
- b. Shell without dorsal-anterior sinuation; anterior end broadly rounded (fig. 18). Genital lobe of female weakly developed, inconspicuous.....*C. albicans* Brady 1864
- 6a. Length of ventral margin of furcal ramus not over seven times the least width of the ramus.....*C. sharpei* sp. nov.
- b. Ventral margin of ramus at least eight times the least width of the ramus....7
- 7a. Length of dorsal seta of furca more than four times the least width of the ramus and longer than the subterminal claw.....*C. crogmaniana* Turner 1894
- b. Length of dorsal seta four times or less than four times the least width of the ramus and shorter than the subterminal claw.....8
- 8a. The terminal claw and more especially the subterminal claw of the furca weakly but distinctly S-shaped (fig. 37-C, T).....*C. sigmoides* Sharpe 1897
- b. The terminal and subterminal claws gently curved, not S-shaped.....9

- 9a. In the third thoracic leg, the shortest seta has a length of over three times that of the ultimate podomere; the companion seta is about equal to or less than twice the length of the shortest distal seta (fig. 53).....10
- b. In the third thoracic leg, the shortest distal seta has a length not over three times that of the ultimate podomere; the companion seta is over twice as long as the shorter of the pair (fig. 45).....14
- 10a. Shell rather elongate with the dorsal margin evenly arched; prominent posterior ventral angulation especially in the left valve (fig. 33).....*C. caudata* Kaufmann 1900
- b. Shell with dorsal margin forming an angulation or sinuation or both (fig. 49).....11
- 11a. Shell height less than one-half the length. Female genital lobe a short cone (fig. 54-G).....*C. suburbana* sp. nov.
- b. Shell height equal to or greater than one-half of the length. Female genital lobe well developed.....12
- 12a. Tip of female genital lobe unevenly bifurcated (fig. 30-G). Posterior end of shell evenly rounded; prominent posterior-dorsal sinuation (fig. 29).....*C. distincta* Furtos 1933
- b. Tip of genital lobe pointed. Posterior end of shell not evenly rounded, subtruncate; posterior-dorsal sinuation lacking or shallow.....13
- 13a. Female genital lobe lappet-like and separated from the thorax (fig. 69-G). Shell without markings on the posterior slope; prominent posterior-ventral angulation (fig. 65).....*C. acuta* sp. nov.
- b. Female genital lobe finger-like, not separated from the thorax (fig. 62). Sculpturing on posterior slope of female shell (fig. 59); juncture of posterior and ventral margin of shell rounded (fig. 58)....*C. fossulensis* sp. nov.
- 14a. In the second thoracic leg, antepenultimate podomere at least equal to the penultimate (fig. 44). Companion seta of third thoracic leg equals two and one-half times the shorter of the pair (fig. 45).....*C. indigena* sp. nov.
- b. The second thoracic leg with the antepenultimate podomere equal in length to two-thirds of the length of the penultimate podomere. Companion seta of the third leg has a length equal to three and one-half times the shorter of the pair.....*C. recticauda* Sharpe 1897

### Group Rostrata

Shell may be beset with many long hairs; shell often moderately short and high so that in most species the height exceeds one-half the length. The respiratory plate of the first thoracic leg is reduced to two setae (fig. 9-R). The mandibular palp has the medial seta on the distal margin of the penultimate podomere smooth, and the bundle on the antepenultimate podomere consists of three setae. Genital lobe of the female reduced and usually rounded (figs. 5-G, 11-G); if pointed, then short and not projected much posteriorly (fig. 15-G). Penis usually short and wide with the lobes flap-like and lying one over another. Three species of Candona, *C. simpsoni* Sharpe 1897, *C. punctata* Furtos 1933, and *C. fluviatilis* sp. nov. have been placed in this group.

## KEY TO SPECIES OF THE GROUP ROSTRATA IN ILLINOIS

- 1a. Shell height considerably more than one-half the length; the length of the ventral margin of the furca over nine times the least width (fig. 5).....  
.....*C. punctata* Furtos 1933
- b. Shell height equal to or less than one-half the length; the length of the ventral margin of the furca less than nine times the least width (fig. 11)....2
- 2a. Dorsal margin of shell straight and horizontal (fig. 6); surface of shell sculptured (fig. 7).....*C. fluviatilis* sp. nov.
- b. Dorsal margin of shell evenly arched (fig. 12). Shell elliptical; surface of shell smooth.....*C. simpsoni* Sharpe 1897

*Candona punctata* Furtos 1933

(Pl. I, fig. 2-5)

*Candona punctata* Furtos 1933. Furtos, 1933:485-486, pl. 13, figs. 2-8.*Type Locality:* Ohio.

*Description of the Female:* A *Candona* of the Rostrata group. The shell (fig. 2) is much higher than one-half of the length; ventral margin nearly straight with but very slight sinuation; dorsal margin convex and passing into the posterior margin without an interruption in the arc. There is a shallow sinuation between the dorsal and the anterior margins. The anterior margin is more narrowly rounded than the posterior. A view from above was not obtained in the Illinois material but observations of single valves mounted in diaphane indicate a width of about four-fifths the height with sides centrally bulged and narrowed anteriorly and posteriorly, giving the animal, according to Furtos (1933), a spindle-form appearance. The left valve is slightly larger than the right. The valves have numerous long, heavy hairs which come from weakly developed papillae. The hairs are conspicuous along the anterior and posterior margins. The surfaces of the valves are areolated making accurate determination of the muscle scars hazardous. The muscle scars, however, appear to be five in number, arranged in a rosette, and are located subcentrally. The pore-canals are obliterated. A weak hyaline border is conspicuous beyond the margin proper. The dimensions of the valves of the single mature Illinois female are as follows (mounted in diaphane):

RIGHT		LEFT	
Length	Height	Length	Height
0.80 mm.	0.45 mm.	0.83 mm.	0.46 mm.

According to Furtos (1933), the length of the female is 0.85 to 0.90 mm., the height 0.45 to 0.51 mm., and the width 0.37 to 0.42 mm. These measurements exceed slightly the size of the individual from Illinois.

The second podomere of the antennule bears a pair of setae, the longer of which reaches to the seventh or eighth podomere, the shorter only to the fifth or sixth podomere. The third and fourth podomeres of the

antennule are little longer than wide; the penultimate and ultimate podomeres are equal in length, the ultimate being about seven times as long as wide. The penultimate podomere of the antenna has on the inner edge a very short spine at the distal end of the basal one-third and a long seta at the beginning of the distal one-third. This seta reaches almost to the tip of the shortest distal claw of the appendage. The mandibular palp has the medial seta of the penultimate podomere unfeathered and three setae in the bundle on the antepenultimate podomere. The two longest claws of the ultimate podomere of the palp are nearly equal in length and shape. The branchial plate of the maxilla has sixteen rays.

The second thoracic leg (fig. 3) is composed of five podomeres, the second of which is equal to or slightly less in length than the sum of the third, fourth, and fifth podomeres taken together. The medial distal seta of the second podomere is equal in length to the width of the third podomere. The third or antepenultimate podomere is about twice as long as wide and has a seta about equal to or slightly larger than the width of the penultimate podomere. The penultimate podomere is not quite as long as the next proximally situated one but is of the same general shape. The ultimate podomere is much longer than wide. The terminal claw (fig. 3-E) is equal to one and one-third times the sum of the lengths of the three distal podomeres. The third thoracic leg (fig. 4) has the penultimate podomere (fig. 4-P) undivided. The basal podomere has three setae. Third podomere (penultimate) about equal in length to the second and bears a seta which is hardly half as long as the length of the podomere. The ultimate podomere is square; the length of the shortest distal seta is three times the length of the ultimate podomere. The length of the longer companion seta is two and one-quarter to two and one-half times the length of the shorter (fig. 4-C). The oppositely directed seta is about three and one-fourth times as long as the shorter seta of the pair.

The furca (fig. 5) has a nearly straight ventral margin; the dorsal margin is slightly concave. The length of the ventral margin is ten times the least width of the ramus; the terminal claw is two-thirds as long as the ventral margin. The dorsal seta (fig. 5-D) is nearly two and one-half times as long as the least width of the ramus, and is located a distance of nearly twice the least width of the ramus from the subterminal claw. The length of the terminal seta is less than the least width of the ramus. The claws are long, slender, and gently curved with some indication of being fine-toothed. The female lobe is undeveloped (fig. 5-G).

*Description of the Male:* The present writer has observed no males of this species. According to Furtos (1933), the males reach a length of 0.93 mm. and the shape of the shell is very similar to that of the female.

*Remarks:* Most of the above description has been taken from a single

Illinois specimen. The description agrees definitely with that given by Furtos. Through the present writer's description, it is evident that this species belongs to the Rostrata group. Because of the uncertainty of the taxonomic importance which may be attached to different structures, it is not advisable at the present time to point out relationships between *C. punctata* and related European species.

*Ecology:* Furtos (1933) reports *C. punctata* to be "common in temporary and permanent ponds, marshes and lakes. March to May, and November." A single mature female was found by the present writer in a collection made from a swampy pool on March 26, 1939; an immature female was collected from a shady pool in an old stream bed on June 6, 1940.

*Distribution:* This species was originally reported from several localities in Ohio by Furtos (1933). The present writer found a single mature female in a collection of crustacea from Indian Creek Valley near Carbondale, Jackson Co., Illinois. This collection was made by Mr. F. R. Cagle of the Southern Illinois State Teachers' College and sent to Dr. Victor Sprague from whom the writer obtained the material. An immature individual was obtained in a collection from Hardin County, Illinois.

*Candona fluviatilis* sp. nov.

(Pl. I, figs. 6-9; pl. II, figs. 10-11)

*Type Locality:* Illinois.

*Description of the Female:* A *Candona* of the Rostrata group. The shell is somewhat compressed; the width is less than the height. The valves (fig. 6) of sexually mature females range in length from 0.68 mm. to 0.76 mm. and in height from 0.33 mm. to 0.38 mm., the length being approximate to twice the height. The dorsal margin of the shell is straight, nearly horizontal; the anterior end is evenly rounded, a situation occurring between the anterior and the dorsal margins. The posterior end is rather blunt with a flattened margin. The ventral margin is centrally somewhat concave. The ovary is slender; the muscle scars (fig. 7-M) are subcentrally located and consist of a rosette of five scars with a single slightly more dorsally located scar and often another scar anterior to the group. The submarginal line is so close to the valve margin that the pore-canals are practically obliterated anteriorly and posteriorly. The shell is conspicuously sculptured (fig. 7-S), being entirely covered by areolations formed of pits separated by raised areas. Many very fine, short hairs are found on the surface and margins of the shell.

The antennules present few specific characters; the third and fourth podomeres are as wide as long, the fourth appears fused to the fifth; the fifth, sixth, and seventh podomeres are stouter and shorter than in many

Candona; the distal podomere is three times as long as wide. The sensory organ (fig. 8-S) of the penultimate podomere of the antenna reaches to the distal margin of the podomere. The ultimate podomere is about one and one-half times as wide as long; the longest claws of the penultimate and ultimate podomeres are as long as the sum of the lengths of the distal three podomeres of the appendage. The teeth of the mandible are long and finger-like, few in number. The medial-distal seta of the penultimate podomere of the palp is smooth; there are three setae in the bundle on the antepenultimate podomere of the mandibular palp. The branchial plate of the maxilla has twenty-three rays, five of which are directed orally. Details of the first thoracic leg are shown in the figure (fig. 9). The second thoracic leg has the distal setae of the second, third, and fourth podomeres approximately equal to the distal width of the respective podomere. The ultimate podomere is longer than wide and bears, in addition to the long claw, two setae, the shorter of which is about as long as the width of the distal end of the podomere, the other approximately equal in length to the proximal margin of the podomere. The length of the terminal claw of the second leg is one and one-third times the sum of the lengths of the three distal podomeres.

The basal podomere of the third thoracic leg (fig. 10) has three setae; the penultimate podomere (fig. 10-P) is undivided. The ultimate podomere is at least as wide as long; the short seta measures two and one-half to three times the length of the podomere, the companion one is two and one-fourth to two and one-half times as long as the short seta, and the oppositely directed one is but little longer, if any, than the other long seta. The seta of the penultimate podomere is seven-eighths as long as the podomere. The furcal ramus (fig. 11) is rather stout and little curved, the length of the ventral margin is approximately six times the least width; the dorsal seta is subequal to twice the least width of the ramus and is located from the subterminal claw a distance equal to the least width of the ramus. The claws are slender, gently curved, and nearly equal in length; the terminal one has a length equal to six-sevenths of the ventral margin of the ramus. The teeth of the claws are so fine that superficially they appear smooth. The length of the terminal seta is approximately equal to one-half of the least width of the ramus. The female genital lobes (fig. 11-G) form large, well rounded semicircular flaps which extend posterior to the furcal rami when the furca is flexed. No seta is found on the thorax dorsad to the furca.

*Male:* The male is unknown.

*Remarks:* The combination of characters found in this species makes comparison with other species of the group *Rostrata* more or less worthless until more information is available regarding the details of anatomy of the American forms.

*Ecology:* *C. fluviatilis* has been taken in only three collections, all of which were from small vernal streams not over three feet wide and ten inches deep, with clear, gently flowing water usually over a muddy bottom.

*Distribution:* Several mature individuals of *C. fluviatilis* sp. nov. were taken on June 20, 1940, near Roberts, Ford County; a single individual was taken on May 18, 1940, near Savoy, Champaign County; and three very immature specimens were collected near Henry, Marshall County, Illinois on May 30, 1940.

Cotypes are deposited in the U. S. National Museum (Cat. No. 81066), in the collection of Dr. H. J. Van Cleave, and in the writer's collection.

*Candona simpsoni* Sharpe 1897

(Pl. II, figs. 12-17)

*Candona simpsoni* Sharpe 1897. Sharpe, 1897:452-454, pl. 46, figs. 1-6; Kofoid, 1908:258.

*Candona reflexa* Sharpe 1897. Sharpe, 1897:457, pl. 47, figs. 1-3; Kofoid, 1908:258.

*Candona exilis* Furtos 1933. Furtos, 1933:483, pl. 12, figs. 14-17.

*Type Locality:* (*C. simpsoni*) Illinois; (*C. reflexa*) Havana, Illinois; (*C. exilis*) Ohio.

*Description of the Female:* A *Candona* assignable to the Rostrata group. The shell (fig. 12) is, in general, elongate-elliptical, two and one-fourth times as long as high, well rounded anteriorly, rounded or a little pointed posteriorly. The dorsal margin is weakly arched; the ventral margin slightly sinuated. From above, the width is approximate to the height, the outline of the shell is subelliptical, and the anterior part is somewhat more pointed than the posterior. The valves are slightly beset with hairs, each hair being set on a rather prominent papilla. Although the shape and the actual size of the shell varies considerably, the length to height ratio seems to remain rather constant. Sharpe (1897) gives the size for *C. simpsoni* as follows: 0.73 mm. long, 0.30 mm. high, and 0.29 mm. wide. Furtos (1933) in describing *C. exilis* gives the length as 0.81 mm., height as 0.38 mm., and width as 0.37 mm. The dimensions given by Furtos are near the largest size found by the writer. Measurements of several valves from Illinois specimens are as follows (mounted in diaphane):

RIGHT		LEFT	
Length	Height	Length	Height
0.78 mm.	0.36 mm.	0.80 mm.	0.— mm.
0.72	0.33	0.74	0.34
0.73	0.33	0.75	0.34

Sharpe (1897) mentions that the antennae of the female are "shorter and thicker than usual" and this holds true in most individuals but there

is a slight tendency for the antennae to become more elongate in individuals which have nearly straight, slender furcal claws. The medial seta of the penultimate podomere of the mandibular palp is smooth; three setae form the group on the antepenultimate podomere of the mandibular palp. The second thoracic leg consists of five podomeres, "terminal segment conical, approximately as long as the penultimate, which is about as wide as long; antepenultimate segment like the penultimate,—the three combined being but an eighth longer than the second segment. Terminal claw as long as the last three segments" (Sharpe, 1897). In many individuals, the three distal podomeres of the second thoracic leg are a little longer than wide; the entire leg is more slender than shown by Sharpe (1897:pl. 46, fig. 5).

The penultimate podomere of the third thoracic leg (fig. 13) is undivided. In the individuals which closely approach the original description of *C. simpsoni*, the penultimate podomere bears several minute spines scattered over the surface. These are not always conspicuous. The ultimate podomere is as wide as long. The shortest distal seta is about two and one-half times as long as the length of the ultimate podomere. Sharpe (1897:pl. 46, fig. 2) shows the shortest distal seta as being straight; Furtos (1933) states that the seta is sharply bent near the tip in *C. exilis*. Individuals which show either straight or bent setae are common; a few individuals have been observed in which the seta is recurved. Individuals may also be found with the "reflexa" type of strongly bent seta. In relation to the shortest distal seta, the companion seta is two to nearly three times as long and the oppositely directed seta is about three times as long.

The furca (figs. 14, 15, 16) is extremely variable especially in regard to the shape of the terminal and subterminal claws. In general, the length of the furca is between six and eight times the least width of the furcal ramus. The dorsal seta is always long, being usually twice the least width of the ramus, occasionally a little longer. It may be abruptly bent dorsally near the distal end and is removed from the subterminal claw an average of one-fourth the length of the dorsal margin of the furca. The length of the terminal seta is usually about one-half the least width of the ramus, but in a few individuals may be nearly as long as the least width of the ramus. The length of the terminal claw is from one-half to two-thirds the length of the furcal ramus. The terminal claw may vary from rather stout to slender and is more or less curved near the tip. Both subterminal and terminal claws are toothed, the teeth usually appearing very prominent in the center of the proximal one-half of each claw. An extreme amount of variation is shown in the subterminal claw. In the individuals described by Sharpe (1897:pl. 46, fig. 6), the subterminal claw is decidedly S-shaped (fig. 14). Furtos (1933:pl. 12, fig. 17) shows this struc-

ture in *C. exilis* as having at the most only a very slight tendency to be S-shaped (fig. 15). The writer has seen both of these shapes represented in his Illinois material with a perfect transition between the two. In addition, the writer has observed individuals in which the subterminal claw is very long and slender with the proximal portion straight and the distal portion only slightly curved (fig. 16). The female genital lobe (fig. 15-G) is poorly developed. It is represented by a small and slightly posteriorly extended thoracic process.

*Male:* The male is not mentioned by Sharpe (1897, 1918). Furtos (1933) states that the male is unknown. The present writer has seen no mature males assignable to *C. simpsoni*. However, a few uncertain immature males with entirely undeveloped copulatory organs have been noticed in collections containing mature females of *C. simpsoni*. These doubtful individuals were too incompletely developed to make certain any identification or to merit description at this time.

*Remarks:* *Candona simpsoni* is the most variable species of ostracod observed by the writer. It is only through a very large series of collections that such variation can be studied. A study of single, isolated individuals instead of a series might lead, in the instance of this species, to the description of three or possibly four species. Through observations made upon material from sixty different localities, it has been possible to determine the variation existing in this species and to demonstrate that the series representative of the species is definitely without any sufficient break to allow even the recognition of subspecies.

The most constant characters are size and shape of the shell. Beyond this, most of the structures usually considered to be of specific importance are very variable. The variability of the appendages lies chiefly in the relative length of the entire appendage and its parts. The writer applied statistical methods to a study of thirty individuals, representing all shapes of the subterminal furcal claw. Measurements were made of eight different structures of the second and third thoracic legs and the furca. From these data, ratios were figured between the following measurements: the length of the claw and the length of the ultimate podomere of the second leg, the length of the short seta and the length of the ultimate podomere of the third leg, the length of the dorsal seta and least width of the furcal ramus, and the length of the terminal claw and least width of the furcal ramus. In every instance except one, an unimodal curve resulted when frequency distributions of the ratios were plotted. The one exception was the frequency curve of the ratio of the dorsal seta of the furca and the least width of the ramus. This was a bimodal curve but there was no correlation whatever between the two peaks of the curve and the type of subterminal claw. From these data, the writer believes that he is justified in stating that the unimodal nature of the curves indicate conclusively the

presence of a single species among the diversified individuals measured. Moreover, the actual measurements of the various structures (length of ultimate podomere and length of the claw of the second leg; length of ultimate podomere and short seta of the third leg; and the least width, length of the dorsal seta, and length of the terminal claw of the furca), the distribution in Illinois, the type of habitat, and the dates upon which the collections were made show no correlation whatever with the shape of the subterminal claw of the furca.

Adequate transition individuals occur in which the animal displays characters of both *C. simpsoni* of Sharpe and *C. exilis* of Furtos. In many instances, the transition is self-sufficient to prove conclusively that both of these species are the same. In one individual, there was found an S-shaped subterminal claw on one side of the body and a claw of the "exilis" form on the other side. Again, in an individual in which were found straight furcal claws as shown in figure 16, the antennae were stout and there were small spines on the sides of the penultimate podomere of the third thoracic leg (fig. 13) as is characteristic of the form "simpsoni." This individual had the shell size and distinctly curved short distal seta of the third leg described for the "exilis" form. Thus in some individuals, combinations of characters may be found which definitely unite the variable individuals into a single species. It is as easy to find an individual with a curved short distal seta on the third thoracic leg in the "simpsoni" form as it is in the "exilis" form, or for that matter in the form with straight claws; the small spines on the penultimate podomere of the third leg may also be found in all three forms if sufficient numbers of individuals are examined. There seems to be no correlation between the curved distal seta and the small spines mentioned above, and indeed no correlation with either of these and the type of furcal claw. Transitions also occur between *C. simpsoni* and *C. reflexa*. In some of the transitions, there may be found a short bent seta on the third leg as Sharpe described for *C. reflexa* and a typical S-shaped subterminal claw as found in *C. simpsoni*.

Whether or not there exists races with all of the individuals showing one type of furcal claw is not now certain. Such a problem involving the examination of large numbers of individuals from different localities would merit investigation. In general, ordinary field collections as made by the writer contain too few individuals for population analyses.

In regard to the placement of *C. simpsoni* in the proper group of the genus Candona, the writer assigns this species to the group Rostrata because there are three setae in the bundle on the antepenultimate podomere of the mandibular palp and because the female genital lobe is poorly developed. However, the shell length is slightly greater than twice the height and the valves are relatively smooth, this being contrary to the

typical condition in the Rostrata group. This would tend to exclude this species from the group. The writer holds the opinion, however, that more consideration and weight should be given to the condition of the genital lobes of the female than to the ratio of height to length of shell. This is also apparently the opinion of European writers.

*Ecology:* Sharpe (1918) reports that *C. simpsoni* is a bottom form of lakes and river shores, and also ponds, while Furtos (1933) gives the habitat as "shallow weedy ponds and marshes." The majority of the writer's seventy collections of this species were made in grass or in masses of algae along the edge of ponds and sluggish streams. One individual was taken from the water in a crayfish burrow. The young of *C. simpsoni* may be taken from ponds before the prevernal break-up of the surface ice. Young individuals may be taken through much of the aestival season; the adults persist through autumn in habitats that do not dry up during the summer. In general, the individuals of this species are not taken in great numbers in most collections. Collections with as many as ten individuals, however, are not rare. In only two of the writer's seventy collections was this species found in numbers greater than ten. One of these collections contained twenty, the other about one hundred individuals. This last collection was made from a temporary pond in Woodford County, Illinois.

*Distribution:* *Candona simpsoni* appears to be the most common and widely distributed Candoninae in Illinois. Sharpe (1897) reported it from Havana and Urbana, Illinois. Kofoid (1908) also reported it from Havana, Illinois. The writer has taken it in collections throughout the state from Lake County on the north to Hardin and Johnson Counties on the south. Furtos furnishes the only record outside of Illinois in her reference (1933) to *C. exilis* in Ohio.

### Group *Compressa*

More than three setae in the bundle on the inner margin of the antepenultimate podomere of the mandibular palp. Otherwise as in group Rostrata.

Only two species assignable to the group *Compressa* are known from Illinois: *C. albicans* Brady 1864 (*C. parallela* G. W. Müller 1900) and *C. biangulata* sp. nov.

### KEY TO SPECIES OF THE GROUP COMPRESSA FROM ILLINOIS

- a. Dorsal margin of shell straight without a sinuation between it and the anterior shell margin (fig. 18); anterior margin of shell broadly rounded; length of shortest distal seta of third leg is a little over twice the length of the ultimate podomere (fig. 19); length of terminal seta of furca less than the least width of the furcal ramus (fig. 20).....*C. albicans* Brady 1864

- b. A sinuation between the dorsal and anterior shell margins (fig. 24); anterior margin of shell narrowly rounded; length of the shortest distal seta of third leg over three times the length of the ultimate podomere (fig. 27); terminal seta of furca equal to least width of ramus (fig. 28).....*C. biangulata* sp. nov.

*Candona albicans* Brady 1864

(Pl. II, figs. 18-23)

- C. albicans* Brady 1864. Brady, 1864:61, pl. 4, figs. 6-10; 1868:381-2, pl. 25, figs. 20-25 and pl. 36, fig. 12; Sars, 1928:82-83, pl. 39, fig. 1.  
*C. parallela* G. W. Müller 1900. G. W. Müller, 1900:25, pl. 5, figs. 5, 6, 18, 19, 23-25; Sharpe, 1908:401-402, pl. 51, fig. 1-5; 1918:825, figs. 1297a, b, c, d; Furtos, 1933:486-487, pl. 12, figs. 18-20; Dobbin, 1941:241, pl. 3, figs. 11-13.

*Type Locality:* British Isles.

*Description of the Female:* *Candona albicans* of the *Compressa* group has a shell (fig. 18) sub-oval in lateral view. The dorsal margin is nearly straight, sometimes slightly sinuated, and almost horizontal, being nearly parallel to the ventral margin though often inclined somewhat posteriorly. The anterior margin is broadly rounded, the posterior is bluntly rounded. The greatest height is at the beginning of the posterior one-fourth of the shell and is more than one-half of the length. Measurements of the valves of two mature females from Illinois show a considerable variation in actual shell size (mounted in diaphane). These measurements are as follows:

RIGHT		LEFT	
Length	Height	Length	Height
0.84 mm.	0.44 mm.	0.85 mm.	0.48 mm.
0.78	0.42	0.78	0.44

In dorsal view the shell appears elongated with the greatest width in the middle and somewhat less than the height. The posterior margin is rounded and the anterior is somewhat pointed when viewed from above. The valves show many hairs, especially along the anterior and posterior margins. The shell is covered with small pits, and this areolation is especially marked in the anterior and posterior thirds of the shell and in young individuals.

The two longest claws of the penultimate podomere of the antenna extend beyond the tip of the longest claw of the ultimate podomere. The mandibular palp has a smooth medial seta on the penultimate podomere and a bundle of four setae on the antepenultimate podomere. The penultimate podomere of the third thoracic leg (fig. 19-P) is divided, the shortest apical seta is slightly longer than twice the length of the ultimate podomere in American forms and slightly less in European specimens. The seta of the penultimate podomere is also longer than

in the European form. The furca (fig. 20) has a nearly straight posterior margin; both claws are somewhat bent throughout their length. The length of the ventral margin of the furcal ramus is between seven and eight times the least width; the length of the dorsal seta is over two times the least width of the ramus in Illinois specimens but less in the European. The terminal claw is less than one-half of the length of the furca while the terminal seta has a length less than the least width of the ramus. The genital lobe is not well developed; though inconspicuous, it has a hemispherical shape.

*Description of the Male:* The single male of *C. albicans* collected in Illinois has a shell (fig. 21) somewhat similar to that of the female but larger. The right valve measures 0.94 mm. long and 0.48 mm. high; the left valve slightly larger. The valves are not as high in relation to the length as in the female and the dorsal margin is not so flattened or horizontal. The right, but not the left, valve has a slight sinuation at the anterior end of the dorsal margin. The antenna, mandible, and thoracic legs are much as they are in the female. The length of the ventral margin of the furca is ten to eleven times the least width, being much more slender than in the female. The claws and the dorsal setae are also proportionally larger than in the female. The prehensile palps are slightly unequal but nearly similar. The left (fig. 22a) has a rather straight slender distal portion while the right (fig. 22b) is more falciform and stouter than the left. The penis (fig. 23) has less chitinized lobes than in many *Candona* species. The lobes are very flap-like and flimsy in appearance.

The occurrence of males is considered to be rare in this species. Furtos (1933) reports the male as being unknown. Sars (1928) reports that males are rare. He gives a description of the male whose shell differs little in size and shape from the shell of the female. The penis and prehensile palps of the male are said by Sars (1928) to be similar to those of *C. stagnalis* G. O. Sars 1891 in which the penis has "three well defined terminal lappets of nearly equal size, though somewhat differing in shape" (Sars, 1928) and the prehensile palps are unequal and dissimilar, the left being fairly straight and the right subfalcate (Sars, 1928:pl. 38, fig. 2).

*Remarks:* The *C. albicans* found by the writer agrees in most details with the European descriptions and is identical with the Ohio specimens described by Furtos (1933). The short apical seta of the third thoracic leg and the dorsal seta of the furca as well as the seta of the penultimate podomere of the third leg are longer than shown in the descriptions by European writers. The figures given by Sharpe (1908:pl. 51, figs. 3 and 5) for *C. parallela* are very close to the specimens found by Furtos in Ohio and those collected by the present writer. Apparently there is a slight

consistent difference between the European and the American forms. Until larger numbers of individuals are examined from many different localities, it is thought unwise to assign any new specific or even varietal designation to the American form.

For forty years the species under discussion has been known almost universally as *C. parallela* G. W. Müller 1900. After a thorough examination of the description of *Candona albicans* Brady 1864 (Brady, 1868), there is little doubt in the writer's mind that the species described by Brady in 1864 is the same as the one described by G. W. Müller in 1900. The chief apparent difficulty in establishing synonymy between *C. albicans* and *C. parallela* seems to be the smaller size of the former. In spite of this difference, a result of Brady possibly basing his description on immature individuals, Sars (1928) proves almost conclusively that *C. albicans* is the valid name. His arguments are founded on structural resemblances as well as surface sculpturing. Disregarding Sars's demonstration of the validity of *C. albicans*, Klie (1938a) tenaciously holds to the name *C. parallela*; he gives, however, *C. albicans* as a synonym of *C. parallela*. To retain *C. parallela* as the valid name under these circumstances is contrary to law of priority in the rules of nomenclature. Beyond all doubt, *C. albicans* is the valid name and must be retained for this species.

*Ecology:* The habitat of this species in North America seems to be identical with the habitat as recorded for Europe. Sars (1928) reports it as being common in small ditches and pools with muddy bottom. Klie (1938a) gives the habitat as temporary pools with muddy bottom and rich plant growths. Sharpe (1918) reports the habitat as "swampy ponds"; Furtos (1933) found the species in temporary and permanent pools and swamps in Ohio. The present writer secured some of his specimens from a small pool four feet in diameter and not over ten inches deep located just a few feet from the edge of Lake Vermilion at Danville, Illinois, on April 28, 1940. The bottom of the pool was of mud and grass was growing around the edge. Other collections of this species were made in July from temporary streams. *C. albicans* seems to be distinctly a vernal and early aestival form. The males are herein for the first time reported from North America. From the sparsity of the males, it is probable that reproduction in this species is almost entirely parthenogenetic.

*Distribution:* *C. albicans* has been reported from continental Europe and from the British Isles by numerous writers. That it is probably distributed widely in the United States is shown by the report from Colorado by Sharpe (1908), from Ohio by Furtos (1933), and from California by Dobbins (1941). It was obtained by the writer in four collections from Illinois: one from Vermilion County on April 28, 1940, and three from Carroll County on July 5, 1940.

*Candona biangulata* sp. nov.

(Pl. II, figs. 24, 25; pl. III, figs. 26-28)

*Candona acuminata* Sharpe 1897 (*non* Fischer 1851). Sharpe, 1897:449-451, pl. 44, figs. 5-7.*Type Locality:* Illinois.

*Description of the Female:* A *Candona* of the *Compressa* group. From the side, the shell (fig. 24) is elongated; height slightly greater than one-half of the length. The greatest height of the shell is at the posterior end of the flattened dorsal margin. The right valve shows a ventral margin with a slight, even sinuation most marked near the center of the margin. The dorsal margin is very slightly concave, very slightly convex, or in most shells straight. Between the dorsal margin and the anterior margin is a pronounced sinuation. The anterior margin is narrowly rounded. A shallow sinuation lies between the dorsal margin and the posterior margin and in some individuals may be more or less obliterated. The posterior margin is rather broadly curved with a tendency for the arc to become slightly straightened on approaching the ventral margin. The left valve differs in shape distinctly from the right valve although the ventral margin is somewhat similar. The dorsal margin is convex and the sinuations between the dorsal margin and the anterior and posterior margins are not noticeable but may be expressed by a slightly flattened area near both ends of the dorsal margin. The left valve is slightly larger than the right, the height especially being greater. The subcentrally located muscle scars are six in number and display a definite arrangement in all the individuals examined. A single, oval to elongate isolated scar is dorsal to a group of five circular to oval scars arranged in an imperfect rosette. The ovary appears as an elongated, narrow band and reaches the level of the muscle scars. The pore-canals are very short and inconspicuous because the submarginal line is removed but a short distance from the shell margin. The valves are nearly devoid of hairs, though a few bristle-bearing puncta are scattered over the surface. The hairs of the anterior and posterior margins are short and weak. Measurements of the valves of three mature females from Illinois are as follows (mounted in diaphane):

RIGHT		LEFT	
<i>Length</i>	<i>Height</i>	<i>Length</i>	<i>Height</i>
0.71 mm.	0.36 mm.	0.73 mm.	0.— mm. (holotype)
0.70	0.35	0.72	0.38
0.70	0.36	0.71	0.38

A dorsal view of the shell was not obtained but observations of mounted valves indicate that the width of the shell is probably one-fourth to one-fifth less than the height.

The antennules are composed of eight podomeres. The third and

fourth podomeres have a length approximate to the width. The distal four podomeres are much longer than wide, especially the ultimate podomere which is in the form of an elongated cylinder. The third podomere has a short seta equal to the width of the podomere; the fourth has no seta; the fifth has two long swimming setae; and the sixth has, in addition to two long swimming setae, a short seta equal to the width of the podomere. The seventh podomere has two long swimming setae and two short ones slightly less in length than the length of the podomere. The apical setae consist of a short, heavy seta equal in length approximately to the length of the ultimate podomere and two long swimming setae. The antennae consist of five podomeres. The medial side of the third (antepenultimate) podomere bears in addition to the regularly occurring sensory bristle a pair of setae, each slightly longer than the sensory bristle and separated from the distal margin of the podomere by a distance equal to one-half of the width of the podomere taken at the base of the setae. The penultimate podomere is shorter than the antepenultimate and bears two medial setae, one close to the distal margin and the other located proximally a distance equal to the width of the podomere. The penultimate podomere also has a short lateral seta close to the beginning of the distal one-third of the podomere. The ultimate podomere has a width slightly greater than one-half the distal width of the penultimate podomere. The longest claws of the penultimate podomere are equal to or extend slightly beyond the longest claw of the ultimate podomere. The teeth of the mandible are long and pointed; the mandibular palp (fig. 25) is characteristic of the *Compressa* group as the median seta on the penultimate podomere is unfeathered and there are four setae in the group (fig. 25-B) on the antepenultimate podomere. Eighteen rays are present on the branchial plate of each maxilla. The penultimate podomere of the palp of the maxilla is twice as long as the width measured in the distal one-third where the podomere is considerably widened.

The second thoracic leg (fig. 26) has a very large, heavy second podomere (fig. 26-A) whose length is equal at least to the combined lengths of the three more distal podomeres. The antepenultimate podomere and the penultimate podomere are subequal in length; the ultimate podomere (fig. 26-U) is conical with the length slightly greater than the width of the base. The second podomere has a short subterminal seta equal to the distally placed seta of the third or antepenultimate podomere. The seta of the penultimate podomere is approximately as long as, or longer than, the length of the last podomere. The claw (fig. 26-C) of the ultimate podomere is one and one-fourth to one and one-half times the combined length of the last three podomeres. The ultimate podomere also has two short setae, one of which is shorter than the length of the

distal podomere, the other somewhat longer. The third thoracic leg (fig. 27) has five apparent podomeres as the penultimate podomere is clearly divided. The apparent penultimate podomere bears a seta considerably greater in length than the length of the podomere. The ultimate podomere is nearly square in lateral view; the shortest distal seta is longer than the seta of the penultimate podomere and is over three times the length of the ultimate podomere. The longer distal seta of the pair is over one and one-half as long as its shorter companion and is about equal in length to the combined lengths of the three apparent distal podomeres of the third leg. The third distal seta is about one and one-fourth the length of the longer seta of the pair, although considerable variation is shown in the length.

The furca (fig. 28) has a relatively straight dorsal margin; the dorsal seta stands at the apex of a slight convexity; a small indentation in the dorsal margin between the proximal one-half and one-third of the dorsal margin indicates the deepest point in a slight concavity. The ventral margin of the furca is slightly but evenly curved. The least width of the ramus is equal to about one-seventh of the ventral margin. The dorsal seta has a length about two and one-half to three times the least width of the ramus and is located from the base of the subterminal claw a distance of at least twice the least width of the ramus. Both the subterminal and the terminal claws are similar in appearance, being gently curved, long, and slender. The subterminal claw is about six-sevenths as long as the terminal, while the terminal claw is more than one-half and less than two-thirds as long as the dorsal margin of the ramus. No indication of teeth or hairs could be found on the claws although observations were made under high magnification on both diaphane and glycerine mounted materials. The terminal seta is equal to the least width of the ramus. The female genital lobe (fig. 28-G) is small and cone-shaped; often it is distally drawn out papilla-like. The lobe does not extend posteriorly beyond the margin of the furcal rami.

*Male:* The male is unknown.

*Remarks:* It is rather difficult to compare *C. biangulata* sp. nov. with other forms of the group *Compressa* because of the imperfect nature of the literature concerning the external morphology of many forms. In only three previously reported species belonging to the *Compressa* group, as far as the writer has been able to determine, have four setae been definitely reported in the mandibular bundle. These species are: *C. albicans* Brady 1864, *C. hertzogi* Klie 1938 (Klie, 1938d), and *C. bilobata* Klie 1938 (Klie, 1938c). Of these three, *C. albicans* alone has a divided penultimate podomere in the third thoracic leg and, as a result, it is apparently related to *C. biangulata*. One of the species which has a questionable

number of setae in the mandibular bundle and which may be related to *C. biangulata* is *C. aemonae* Klie 1935 (Klie, 1935). Klie does not know for certain whether the bundle of setae on the antepenultimate podomere of the mandibular palp in *C. aemonae* has four or five setae. The third thoracic leg, the furca, and in part the genital lobe are similar to *C. biangulata*. Both *C. biangulata* and *C. aemonae* have two setae on the basal podomere of the third leg. On the other hand, the shape of the shell differs greatly in the two species. Whether or not the two species are closely related must await the determination of the number of setae in the bundle on the mandibular palp in *C. aemonae*.

The writer believes that the ostracod described by Sharpe (1897) under the designation of *C. acuminata* was not the *C. acuminata* of Fischer. That Sharpe himself realized his error is evident from the fact that he later (1918) does not give Illinois as a locality for *C. acuminata* Fischer. Although the shell described by Sharpe is slightly larger than that of *C. biangulata*, there is so much similarity between the description given for *C. acuminata* by Sharpe and the individuals of the present new species, that there can be little question but that they are the same. The present writer gives an entirely new description without reference to Sharpe's description because it is possible that Sharpe's description may be contaminated from European descriptions of *C. acuminata* Fischer.

*Ecology:* This species has been taken by the writer in five collections, each containing only one or two individuals. Two collections were from temporary streams, two from vernal ponds. The fifth collection was secured from water in a crayfish burrow. Sharpe (1897) collected his material from a pond. Obviously, this species lives in temporary waters where there is little or no current. It is usually found over a mud bottom.

*Distribution:* *C. biangulata* sp. nov. was secured by the writer from Champaign, McLean, Will, and Henry Counties, Illinois. Sharpe (1897) reported this species as *C. acuminata* from Clifton, Iroquois County, Illinois on May 12, 1882.

The holotype (female) of this species is deposited in the U. S. National Museum (Cat. No. 81067). One paratype (female) is in the collection of Dr. H. J. Van Cleave and others (female) are retained in the writer's collection.

#### *Group Acuminata*

Shell compressed, width usually about one-third of the length; height often but not always less than one-half the length; posterior end of shell broadly rounded (fig. 49) or obliquely subtruncate to truncate (fig. 40). Shell with few hairs. The medial seta of the penultimate podomere of the mandibular palp smooth; the bundle on the antepenultimate podomere

consists of four setae (fig. 43-S). The female genital lobe is well developed, pointed, and extends posteriorly between the furcal rami (figs. 32-G, 37-G). Outer lobe of the penis usually well developed and conspicuous (figs. 48-O, 57-O).

The group *Acuminata* appears to have reached a high degree of development in North America where there are many more species than in Europe. The exact number of North American species assignable to this group is unknown because the knowledge regarding the minute structure of many species is incomplete. The deficiency of information is especially acute in regard to the number of setae in the bundle on the mandibular palp. It is probable that many of the new species described by Furtos in 1933 belong to this group.

The present writer has definitely assigned eight species from Illinois to this group and two more are assigned tentatively until more details of the structure can be secured. The tentative assignment of these two species, *C. recticauda* Sharpe 1897 and *C. sharpei* sp. nov., is based upon inadequate descriptions.

#### KEY TO SPECIES OF THE GROUP ACUMINATA IN ILLINOIS

- 1a. The antepenultimate podomere of the second thoracic leg is two-thirds as long as the penultimate podomere; the length of the longer companion distal seta of the third thoracic leg is more than three times the length of the shorter one.....*C. recticauda* Sharpe 1897
- b. The antepenultimate podomere of the second thoracic leg as long or longer than the penultimate podomere; the length of the longer companion seta of the third leg is less than three times the length of the shorter of the pair (fig. 53-S).....2
- 2a. Ventral margin of furca not over eight times the least width of the furcal ramus.....*C. sharpei* sp. nov.
- b. Ventral margin of furca over eight times the least width of the furcal ramus.....3
- 3a. Female genital lobe bifurcated, ventral part not as well developed as the dorsal branch (fig. 30-G).....*C. distincta* Furtos 1933
- b. Female genital lobe not bifurcated but drawn out to a single point (fig. 37-G).....4
- 4a. Dorsal margin of shell forms a low arch without conspicuous sinuation or angulation (figs. 33, 36).....5
- b. Dorsal margin of shell forms a high peak usually with, occasionally without, angulations, sinuations, or both (figs. 40, 49).....6
- 5a. Shell longer than 1.10 mm.; ventral margin of furcal ramus eleven times and the dorsal seta two times the least width of the ramus (fig. 35).....*C. caudata* Kaufmann 1900
- b. Female shell less than 1.10 mm. in length; ventral margin of furcal ramus less than ten times and dorsal seta over three times the least width of the ramus (fig. 37).....*C. sigmoides* Sharpe 1897
- 6a. Length of the female shell over 1.25 mm.....*C. crogmaniana* Turner 1894
- b. Length of female shell less than 1.25 mm.....7

- 7a. The dorsal margin of the shell high and rounded (fig. 40); outer lobe of penis distally divided (fig. 48-O); longer companion seta of third leg more than twice the length of the shorter of the pair (fig. 45)...*C. indigena* sp. nov.
- b. The dorsal margin of the shell usually not high and well rounded; outer lobe of penis not distally divided; third thoracic leg with length of the longer companion distal seta equal to or less than twice the shorter of the pair (fig. 53-S).....8
- 8a. Posterior slope of shell of female sculptured (figs. 58, 59); female genital lobe long and finger-like (fig. 62).....*C. fossulensis* sp. nov.
- b. Posterior slope of shell not sculptured; female genital lobe not finger-form...9
- 9a. Shell without posterior-ventral angulation (fig. 49); posterior end of shell rounded; female genital lobe not especially narrowed at junction with the thorax (fig. 54-G).....*C. suburbana* sp. nov.
- b. Shell with posterior-ventral angulation (fig. 65); posterior end of shell subtruncate; female genital lobe narrowed at junction with the thorax (fig. 69-G).....*C. acuta* sp. nov.

*Candona recticauda* Sharpe 1897

*Candona recticauda* Sharpe 1897. Sharpe, 1897:451-452, pl. 46, figs. 7-11; 1918:826, figs. 1299a, b, c, d, e.

*Type Locality*: Clifton, Iroquois County, Illinois.

*Description (after Sharpe, 1897)*: A *Candona* species tentatively assignable to the *Acuminata* group. "Shell of male 1.18 mm. long and .70 mm. high, stout." Both prehensile palps gently bent, the right much heavier than the left and ending in a hyaline point. Terminal claw of the second leg is one and one-half times as long as the sum of the lengths of the distal three podomeres; the antepenultimate podomere is two-thirds as long as the penultimate. The third thoracic leg has the penultimate podomere divided; the ultimate podomere is as long as wide, with the length of the shortest distal seta two and one-half times the length of the ultimate podomere. In Sharpe's figure 7, plate 46, however, the length of this seta appears about one and one-half times the length of the ultimate podomere. The companion seta is about three and one-half times the length of the shorter of the pair. "Caudal rami well developed, long, straight. Terminal claw half as long as the ramus, evenly and gently curved . . . . Dorsal seta three fifths the length of the subterminal claw and at two thirds its length from the claw; terminal seta a third the length of the dorsal one."

*Remarks*: This description by Sharpe appears to be based entirely on males. The present writer has found no specimens which could be identified as *C. recticauda* Sharpe. This species seems related to *C. indigena* sp. nov. from which it differs in the shape of the prehensile claws, the relative lengths of the antepenultimate and penultimate podomeres of the second thoracic leg, and the length of the short seta of the ultimate podomere.

mere of the third thoracic leg. Since Sharpe gives neither a description nor a figure of the shell, accurate identification of specimens belonging to *C. recticauda* may be difficult. For the present, *C. recticauda* should be considered a valid species.

*Ecology:* Sharpe (1897) secured his type specimens from a pond.

*Distribution:* The only available record for *C. recticauda* is that of the type specimens from Clifton, Iroquois County, Illinois (Sharpe, 1897).

*Candona sharpei* sp. nov.

*Candona fabaeformis* Sharpe 1897 (*non* Fischer 1851). Sharpe, 1897:454-455, pl. 45, figs. 1-3.

*Candona fabaeformis* (part?) Sharpe 1897 (*non* Fischer 1851). Sharpe, 1918:826, figs. 1300a, b, c, d.

*Type Locality:* (*C. fabaeformis* Sharpe 1897) Normal, McLean County, Illinois.

*Description (after Sharpe, 1897):* A *Candona* species possibly belonging to the group *Acuminata*. "Length 1.00 mm., height .47 mm., width .49 mm. . . . Seen from the side, it is slightly widest back of the middle, the upper and lower edges nearly parallel, both ends fully rounded, the ventral edge quite deeply sinuate near the middle." Terminal claws of the female antenna scarcely longer than last two podomeres. The penultimate podomere of the third leg divided. "Terminal segment as long as broad, one half as long as the penultimate segment, which is twice as long as broad. Shorter terminal seta twice as long as the terminal segment and a third as long as the longer similarly directed seta; reflexed seta but slightly longer than the longer terminal one." The furca is seven times as long as wide; terminal claw one-third as long as the ramus. The terminal seta is as long as the ramus is wide; "dorsal seta four-fifths as long as the subterminal claw, and distant twice the width of the ramus from it."

*Remarks:* This species, which has been renamed *C. sharpei* sp. nov., cannot possibly be the *C. fabaeformis* of Fischer. G. W. Müller (1912) doubted Sharpe's designation of this form. By the shell width alone, it is possible to see that Sharpe's species is not *C. fabaeformis* Fischer. The species described by Sharpe under *C. fabaeformis* had a shell width of one-half the length while the *C. fabaeformis* of Fischer has a shell width of not over one-third of the length (G. W. Müller, 1900; Klie, 1938a; *et alli*). Also the furca in Sharpe's species is much stouter, having a length of less than seven times the width, while in Fischer's *C. fabaeformis* the furca is elongated and has a length of at least eleven times the least width.

Sharpe apparently studied only female shells as he does not mention the male, and in particular the prehensile claws. However, he pictures the right prehensile claw (1918:fig. 1330d) at a later time. It is entirely possible that this illustration was borrowed from European descriptions of the true *C. fabaeformis*. In regard to Turner's report (1895) of *C. fabaeformis* in Georgia, it is apparent (Cf. G. W. Müller, 1912) from a study of the shell characters that it is also not assignable to *C. fabaeformis* of Fischer. At the same time, it is doubtful if the specimens described by Turner (1895) and Sharpe (1897) belong to the same species as they appear to differ in many respects.

A definite assignment of *C. sharpei* sp. nov. to any certain group of the genus *Candona* is of course impossible. If one knew for certain that Sharpe (1918:fig. 1300d) pictured the right prehensile palp from an Illinois individual, there would be little hesitancy in referring this species to the group *Fabaeformis*. Moreover, assignment to any group is difficult because the condition of the female genital lobe is unknown. In general appearance, the writer suspects that the species probably belongs to the *Acuminata* group and is related to such forms as *C. acuta* and *C. sigmoides*. It is entirely possible that Sharpe based his species diagnosis on immature individuals. At any rate, the writer is of the opinion that *C. sharpei* sp. nov. should be carried in the literature until the *Candoninae* of the state are better known and the variation occurring within species is understood. It may then be possible to place this species.

*Ecology:* Sharpe (1897) reports this species from a pool.

*Distribution:* The only certain reference to *C. sharpei* sp. nov. is that of Sharpe (1897) who reported it under the name *C. fabaeformis* from Normal, Illinois on March 27, 1881.

### *Candona distincta* Furtos 1933

(Pl. III, figs. 29-30)

*Candona distincta* Furtos 1933. Furtos, 1933:478-479, pl. 8, fig. 15; pl. 9, figs. 13-16; pl. 12, figs. 21-22.

*Type Locality:* Ohio.

*Description of the Female:* A *Candona* of the *Acuminata* group (fig. 29). "From the side: elongated, height about one-half the length; extremities rounded, the posterior narrower; ascending slope of the dorsal margin moderately arched, with a distinct sinuation in the middle giving the appearance of two dorsal humps, the posterior of which is the higher; descending slope of dorsal margin almost straight; ventral margin sinuated; submarginal line removed from the mid-central and

posterior margins" (Furtos, 1933). The measurements of valves of two females from Illinois mounted in diaphane are:

RIGHT		LEFT	
Length	Height	Length	Height
0.92 mm.	0.47 mm.	0.93 mm.	0.49 mm.
0.97	0.50	0.98	0.52

The penultimate podomere of the third leg is divided. In the material from Illinois, the shortest distal seta of the third thoracic leg is nearly four times the length of the ultimate podomere while the companion seta is slightly under two and the oppositely directed seta slightly over two times the length of the shortest seta. The ventral margin of the furca (fig. 30) is eight or nine times the least width of the furcal ramus; the length of the dorsal seta is about three times and the length of the terminal seta about one and one-fourth times the least width of the ramus. The dorsal seta is removed from the subterminal claw by a distance equal to three times the least width of the ramus. "Genital lobes moderately developed, proximal portion rectangular, slightly longer than broad, distal process somewhat forked, the ventral branch barely developed" (Furtos, 1933).

*Description of the Male:* "Male larger than the female, left valve larger than the right, projecting beyond it at each extremity, sinuation of dorsal margin less pronounced, ventral margin with a small anterior hump, behind which the sinuation is deeper than in the female" (Furtos, 1933). The sizes of valves of three males from Illinois (mounted in diaphane) are as follows:

RIGHT		LEFT	
Length	Height	Length	Height
1.00 mm.	0.53 mm.	1.01 mm.	0.54 mm.
1.02	0.56	1.04	0.57
1.05	0.55	1.07	0.56

*Remarks:* The Illinois material agrees precisely with the original description of Furtos (1933).

*Ecology:* Furtos (1933) reported this species as common in marshes, canal basins, and small lakes. The present writer collected his specimens from a small temporary prairie pond and a grassy roadside ditch. Like many other *Candona* species, this form is apparently vernal in seasonal distribution.

*Distribution:* Furtos (1933) reported *C. distincta* from several localities in Ohio. The present writer's collections were secured from Seymour Prairie, Champaign County, on April 1, 1940, and from the same vicinity but in Piatt County, Illinois, on May 4, 1940.

*Candona crogmaniana* Turner 1894

(Pl. III, figs. 31-32)

*Candona crogmaniana* Turner 1894. Turner, 1894:20-21, pl. 8, figs. 24-33; Furtos, 1933:476, pl. 8, figs. 1-3; pl. 9, figs. 17-18; pl. 11, figs. 9-10.

*Candona crogmani* Turner 1895. Turner, 1895:300-301, pl. 71, figs. 24-33; pl. 81, figs. 4-5; Sharpe, 1918:824, figs. 1295a, b, c.

*Type Locality:* Atlanta, Georgia.

*Description of the Female:* A *Candona* of the *Acuminata* group. "From the side: elongated, subtriangular, height less than one-half the length, highest in the posterior third; anterior extremity broadly rounded, the posterior narrow; ascending slope of dorsal margin gently arched, with an anterior sinuation, descending slope steep; ventral margin sinuated" (Furtos, 1933). The shell (fig. 31) is large; valves of three mature females from Illinois (mounted in diaphane) measure as follows:

RIGHT		LEFT	
Length	Height	Length	Height
1.32 mm.	0.65 mm.	1.37 mm.	0.68 mm.
1.41	0.68	1.45	0.70
1.28	0.63	1.33	0.65

The mandibular palp has the medial-distal seta of the penultimate podomere smooth and has four setae in the bundle on the antepenultimate podomere. The penultimate podomere of the third thoracic leg is divided; the distal podomere is nearly as wide as long; and the shortest distal seta is four times the length of the distal podomere. The companion seta is two and one-half times as long as its shorter mate, and the oppositely directed seta is three times as long as the shortest distal seta. The furca is gently curved; the ventral margin is twelve to thirteen times the least width. The dorsal seta has a length of over four times the least width of the ramus and is removed from the subterminal claw by a distance equal to almost four times the least width of the ramus. The terminal claw has a length approximate to one-half of the length of the ventral margin of the ramus while the terminal seta has a length approximate to twice the least width of the ramus. The genital lobe (fig. 32-G) consists of a long finger-like projection extending posteriorly and dorsally from a bulbous base.

*Description of the Male:* With the exception that the shell size is slightly larger in the male than in the female and that the shape is somewhat different, the anatomical details of the male and the female are the same. No males were observed by the writer in his material collected in Illinois. The reader is referred to Furtos's description of the male (Furtos, 1933).

*Remarks:* Furtos is correct in assigning to this species the older name

given by Turner instead of the later name, *Candona crogmani*, which Turner tried to introduce in 1895. He probably thought that *crogmani* was a much simpler name and orthographically more correct than *crogmaniana*. The original name must stand, however, as the valid designation for this species.

*Ecology:* Turner (1894) collected the original lot of specimens from shallow ponds near South River, Atlanta, Georgia. Turner (1895) describes these ponds as "drying up in warm weather." Furtos (1933) collected *C. crogmaniana* from both permanent and temporary ponds. The present writer has taken this species along the edge of a permanent pond (ox-bow) both from masses of floating algae and from dead leaves and grass on the bottom.

*Distribution:* *Candona crogmaniana* was collected by Turner (1894) from near Atlanta, Georgia; by Furtos (1933) from several places in Ohio; and by the present writer from near Muncie, Vermilion County, Illinois. The writer's two collections came from Muncie pond on April 28, 1940.

*Candona caudata* Kaufmann 1900

(Pl. III, figs. 33-35)

*Candona caudata* Kaufmann 1900. Kaufmann 1900a:365-368, pl. 24, figs. 16-20; pl. 26, figs. 17-23; Sars, 1928:76-77, pl. 35; Klie, 1938a:68, figs. 223-225.

*Candona elongata* G. W. Müller 1912 (*non* Herrick 1879). G. W. Müller, 1912:140.

*Type Locality:* Switzerland, Europe.

*Description of the Female:* "Shell rather elongate, seen laterally, narrow reniform in shape, with the greatest height not nearly attaining half the length, dorsal margin gently arched, without forming any distinct angular bend either in front or behind, posterior obliquely produced and exerted to a rather prominent peculiarly deflexed corner more fully developed on the left valve, this corner being however quite obsolete in immature specimens;—seen dorsally, narrow elliptical in outline, with the greatest width only slightly exceeding one-third of the length, both extremities obtusely pointed" (Sars, 1928) (fig. 33). Measurements of mature females (valves mounted in diaphane) from Illinois are as follows:

RIGHT		LEFT	
<i>Length</i>	<i>Height</i>	<i>Length</i>	<i>Height</i>
1.26 mm.	0.60 mm.	1.31 mm.	0.63 mm.
1.30	0.60	1.34	0.62
1.26	0.60	1.30	0.61
1.10	0.50	1.13	0.51

The valves are sparsely haired and are marked by minute elevated areas separated by fine grooves. The pore-canals are rather conspicuous.

That this species belongs to the *Acuminata* group is evidenced by the fact that the medial-distal seta of the penultimate podomere of the mandibular palp is smooth and there are four setae in the group on the antepenultimate podomere of the same palp. The antennules and the antennae are stouter and heavier than in many of the *Candona*; the distal claws of the antennae are spine-like and the setae of the antennules are short. The respiratory plate of the maxilla has twenty-two rays or setae, four of which are directed orally. The second thoracic leg has clusters of small hairs and isolated spines along the sides of the second, third, and fourth podomeres. The third thoracic leg (fig. 34) has the penultimate podomere divided; the seta of the penultimate podomere is shorter than the shortest distal seta of the appendage. The ultimate podomere is nearly square; the shortest seta is about four times the length of the ultimate podomere. The longer seta of the similarly directed pair is one and one-half times as long as its shorter companion while the oppositely directed seta is nearly twice as long as the shortest distal seta.

The length of the ventral margin of the furca (fig. 35) eleven times the least width; the length of the dorsal seta twice the least width; and the terminal seta about the same length as the ramus is wide. The terminal claw has a length about equal to one-half of the length of the furca and the dorsal seta is separated from the subterminal claw by a distance approximate to one-third of the length of the ventral margin of the ramus. A short but conspicuous seta is located on the body dorsal to the furca. The genital lobes form a prominent conical lappet.

*Male:* The male is unknown both in Europe and in the material collected by the present writer (*Cf.* Sars, 1928; Klie, 1938a).

*Remarks:* There can be little question but that this is the *Candona caudata* described by Kaufmann. There seem, however, to be a few minor differences between the American specimens and the description given by Kaufmann. The shell of the American form is often slightly higher in proportion to the length. All of the setae of the third thoracic leg appear to be longer in relation to the length of the podomeres in American than in European forms but the ratios between the various setae lengths are about the same. One of the most conspicuous differences between the specimens from Illinois and the original specimens described by Kaufmann (1900a) is in the dorsal seta of the furca. In the type material, Kaufmann describes the dorsal seta as being feathered. The American specimens have a smooth and perhaps a little longer dorsal seta than that described from European material. That the smooth condition is common in Europe, where it is considered of insufficient importance to separate species, is evidenced by both Alm (1916) and Sars (1928) who figure a smooth dorsal seta. As the differences between the American and

European individuals are so slight and within the acknowledged range of individual variability, the writer does not hesitate to place the Illinois specimens in the species *C. caudata* Kaufmann.

A comparison of *C. caudata* with several closely related species is given in the "remarks" under *C. acuta* *sp. nov.*, described herein.

*Ecology:* European writers (Kaufmann, 1900a; Sars, 1928; *et alli*) report *C. caudata* chiefly from canals and lakes. Of the four collections of this species made by the writer, two came from silt bottomed drainage ditches with grass, weeds, and algae along the edge; the third from a permanent pond (ox-bow); and the fourth was taken from the stomach of a fish, *Catostomus commersonii*, taken from the stripland ponds near Oakwood, Illinois.

*Distribution:* *Candona caudata* Kaufmann 1900 is one of the common species of Europe and is well distributed over central and northern Europe as well as the British Isles. The present report is the first from North America. The writer's collections of this species were all from Vermilion County, Illinois.

*Candona sigmoides* Sharpe 1897

(Pl. III, figs. 36-38)

*Candona sigmoides* Sharpe 1897. Sharpe, 1897:455-456, pl. 45, figs. 4-11; Kofoid, 1908:258; Sharpe, 1918:825, figs. 1298a, b, c, d.

*Type Locality:* Mason County, Illinois.

*Description of the Female:* A *Candona* of the *Acuminata* group in which the shell height is nearly equal to one-half of the length. The valves of the shell differ somewhat in lateral view. The left valve (fig. 36) is the larger both in length and height; the greatest height is in the posterior one-third of the valve. The dorsal margin of the left valve is fairly evenly arched passing into the anterior and posterior margins without pronounced sinuation or angulation. The angulation formed by the posterior and ventral margins is distinct and projects somewhat into a weak point, just anterior of which is a slight sinuation of the ventral margin. The anterior end is somewhat narrowly rounded. There is a sinuation in the center of the ventral margin with a convexity located about one-half the distance from the ventral sinuation to the posterior-ventral point. The right valve is somewhat different in shape. There is a well marked sinuation between the dorsal margin and the anterior margin; there is a slight angulation at the juncture of the dorsal and posterior margins and the posterior-ventral point is not as well developed. There is also less of a convexity in the ventral margin between the ventral sinuation and the posterior-ventral point which is very weakly pronounced in the right shell half.

Measurements of the valves of three mature females from Illinois are as follows (mounted in diaphane):

RIGHT		LEFT	
Length	Height	Length	Height
1.04 mm.	0.52 mm.	1.06 mm.	0.56 mm.
1.05	0.52	1.07	0.54
1.02	0.52	1.06	0.54

The shell surface is smooth with a few scattered hairs. These are best developed around the posterior-ventral point and along the anterior margin. The submarginal line is close to the margin so that the pore-canal are very short. There is a group of five muscle scars arranged in a rosette with a single scar just anterior to the group. There are also two pairs of scars: a pair of very small scars located some distance anterior-dorsal from the group, and another pair, each of which is well separated and large, located a little distance anterior and ventral of the group. A view of the shell from above was not obtained.

The antennules are stout with many of the podomeres appearing square in side view; the setae of the antennules are much shorter and heavier than in most Candoninae. The antennae are short and stout. The outer margin of the penultimate podomere of the antenna bears a seta almost in the center of the margin; the antepenultimate podomere bears a pair of medial-distal setae which extend past the base of the distal claws. The mandibular palp has the medial seta on the penultimate podomere smooth and the bundle on the antepenultimate podomere consists of four setae.

In the second thoracic leg, the distal claw is equal to the sum of the lengths of the last three podomeres. The ultimate podomere is more nearly cylindrical than conical and is over one-half as long as the penultimate podomere. The third thoracic leg has the penultimate podomere divided; the ultimate podomere is square and its shortest distal seta has a length nearly four times the length of the podomere. The seta of the penultimate podomere is as long as the sum of the lengths of the apparent penultimate and antepenultimate podomeres and about one-fourth again as long as the shortest distal seta. The distal seta, companion to the shortest one, is about two and one-fourth times as long as the short seta and the oppositely directed one is about the same length as the longer of the pair. The basal podomere of the third thoracic leg has two setae. The furcal rami (fig. 37) are considerably curved; the ventral margin of each measures nine or nine and one-half times the least width. The dorsal seta has a length of three and one-fourth times the least width of the ramus and is located from the subterminal claw a distance equal to three times the least width. The terminal seta (fig. 37-S) has a length

of one to one and one-third times the least width of the ramus. The terminal claw is approximate to one-half the length of the ventral margin of the furca. The claws are stout and in most specimens are slightly S-shaped, especially the subterminal claw (fig. 37-C). The genital lobe is elongated, almost finger-like, and extends posteriorly between the furcal rami (fig. 37-G).

*Description of the Male:* The shell of a mature male measured 1.20 mm. in length and 0.61 mm. in height. Sharpe (1897) gives the size as 1.25 mm. long and 0.63 mm. high. The single intact male shell of the writer's collections agrees with the description given by Sharpe: "the shell of the male is much higher posteriorly, the greatest height being about half the length; anterior extremity evenly rounded, narrow; posterior sloping ventrally. Dorsal margin rather evenly rounded; ventral, deeply sinuate anterior to the middle of the shell" (Sharpe, 1897). As this single mature male with the shell intact had been dead for some time, it was impossible to secure from it any details of the appendages beyond those given by Sharpe (1897). In another male, however, the appendages were in such condition as to allow a comparison with the description given by Sharpe. In addition to the observations given by Sharpe, the writer found that the penis (fig. 38) is oval in shape and widened in the center. The outer lobe is conspicuous; the two distal lobes small. Besides differing in the shape and size of the shell, the male differs from the female chiefly in the shape of the furca which is much straighter and distally narrower in the male.

*Remarks:* While Sharpe based his original description of *C. sigmoides* on male specimens and the present writer found only two mature males for comparison, it is evident especially through the shape of the furcal claws that the females seen by the writer belong to this species. One of the mature male specimens occurred in a collection in which were two mature females as well as several immature young males possibly also belonging to this species, but too insufficiently developed to merit identification or description.

*Ecology:* Sharpe (1918) reports *C. sigmoides* from lake and river shores. The present writer found it in algae hanging in the slow current of a small permanent stream three feet wide and in water plants along the edge of two small sluggish permanent streams.

*Distribution:* Sharpe (1897) collected his specimens of *C. sigmoides* at Havana, Illinois, and Kofoid (1908) reported the species from the same locality. The present writer has taken the species in Lake County on June 29, 1940; in Tazewell County on August 29, 1940; and in Knox County on June 14, 1940. This species has not been reported outside of the State of Illinois.

*Candona indigena* sp. nov.

(Pl. III, fig. 39; pl. IV, figs. 40-48)

*Type Locality:* Illinois and Tennessee.

*Description of the Female:* A *Candona* species of the *Acuminata* group. The holotype (fig. 39) in alcohol measured 1.08 mm. in length, 0.59 mm. in height, and 0.52 mm. in width. The width is little less than 90% of the height. Measurements of left valves of six females including several paratypes as well as the holotype after mounting in diaphane were:

<i>Length</i>	<i>Height</i>
1.04 mm.	0.60 mm. (holotype)
0.96	0.56
0.97	0.58
0.96	0.55
1.00	0.55
1.10	0.65

The right valve (fig. 40) of the shell of the female is not as high as the left, being usually 0.02 to 0.03 mm. less. The anterior margin of the shell is somewhat evenly rounded, blending into the dorsal margin without much conspicuous change in the arc. The highest part of the left shell is at the beginning of the posterior one-fourth in most shells, slightly anterior to this in a few individuals. At the beginning of the posterior one-fourth, a very distinct angulation is formed by the curved dorsal margin and the abruptly subtruncated posterior margin. The posterior-ventral angulation approaches more a right angle than one of sixty degrees. The ventral margin is slightly but distinctly sinuated; the submarginal line is relatively removed from both the posterior-ventral and the anterior-ventral margins; the pore-canals are very conspicuous, especially along the anterior-ventral and the posterior-ventral margins. From above (fig. 42): ovoid, slightly less pointed posteriorly than anteriorly; the left valve slightly overlapping the right at both ends. The sides make a very even and uninterrupted arc; widest in the area just behind the midpoint and considerably posterior to the attachment place of the closing muscles. Bristles of the dorsal posterior margin usually very long and heavy; finer bristles at the ventral posterior margin and along the anterior margin. The surface of the shell bears a few scattered puncta with hairs. The muscle scars are subcentral, usually slightly ventral and anterior from the center of the shell. There is normally a curved anterior row of four scars with two additional scars just posterior to the ventral two of the row. There may be two weak, separated scars ventral and anterior to the group of six.

The antennules consist of eight podomeres; podomere three is distinctly wider than long; podomere four is slightly wider than long, being

much shorter than the more distal podomeres. Podomere five is one and one-half times as long as wide. The ultimate (eight) and antepenultimate (six) podomeres are equal in length to the fifth, while the length of the penultimate podomere is one and one-half the length of the fifth. Antennae of five podomeres in the female. Two of the claws of the penultimate podomere are equal or subequal to the longest one of the claws of the last podomere. The shorter terminal claw is six-sevenths or seven-eighths as long as the other and extends beyond the shortest claw of the penultimate podomere. The ultimate podomere is about three-fifths as wide as long. The teeth of the chewing edge of the mandible (fig. 43-C) are elongated, heavily chitinated, and distinctly separated from each other even at the base. The palp is characteristic of the *Acuminata* group with the seta of the medial side of the penultimate podomere unfeathered and having a group of four setae (fig. 43-S) on the inner margin of the antepenultimate podomere. The branchial plate of the maxilla has twenty-four rays, the first five of which are directed toward the mouth. One seta of the third maxillary process is larger than the rest and not toothed.

The branchial plate (exopodite) of the first thoracic leg is reduced to two setae. One of these is rather stout and over  $60\ \mu$  long, the other is weak and just a little more than one-fourth the length of the first. The second thoracic leg (fig. 44) is composed of five podomeres. Near the apical border of the second podomere is a seta approximately equal in length to the width of the podomere. The length of the second podomere is about equal to the sum of the lengths of the three more distal podomeres. The antepenultimate and penultimate podomeres are subequal in length and each is about five-eighths as wide as long. Each of these podomeres has a seta which is not quite equal in length to the podomere. The penultimate podomere also has a very small seta whose base is near the base of the larger one. The ultimate podomere is conical and tapers evenly to the apical claw. One of the two apical setae is equal in length to the apical podomere and the other is one-half as long. The apical claw is equal in length roughly to one and one-fourth times the sum of the last three podomeres of the appendage.

The third thoracic leg (fig. 45) clearly appears to be formed of five podomeres. There are no setae on the second and the apparent antepenultimate podomeres. The seta of the penultimate podomere and the shortest seta of the ultimate podomere are not more than gently curved and are not bent distally. In relation to the shortest seta of the apical podomere, the companion seta is about two and one-fourth to two and one-half times the shortest in length; while the oppositely directed seta is only two to two and one-fourth times as long. The apical podomere is about as long as wide.

The furcal ramus (fig. 46) of the female has a straight dorsal margin and a slightly curved ventral margin. The ratio of the least width of the base of the furca to the length of the ventral margin is about 1:9. The dorsal seta is three and one-half times the least width of the base of the furca and is removed from the subterminal claw by a distance more than twice the least width of the ramus. The subterminal claw measures in length nearly five times the width of the ramus; while the terminal claw is about one-half of the length of the dorsal margin of the ramus. The terminal seta is small, measuring about one and one-half times the least width of the ramus. Both claws are curved at the tips, rather slender, and are toothed especially in the middle third. The female sexual lobe (fig. 46-G) is moderately developed, being in the form of a narrow cone or papilla extending finger-like between the furcal rami but usually not beyond the dorsal margin of the rami. The ventral margin of this lobe is somewhat concave, while the dorsal margin is nearly straight.

*Description of the Male:* The shell of the male is nearly like that of the female when viewed from above. From the side (fig. 41), however, the ventral margin is usually more concave and the posterior margin is more rounded with a less conspicuous posterior-ventral point. The allotype measured 1.08 mm. long, 0.61 mm. high, and 0.54 mm. wide in alcohol. Measurements of the left valve of two males mounted in diaphane are as follows:

<i>Length</i>	<i>Height</i>
1.04 mm.	0.59 mm. (allotype)
1.04	0.60 (paratype)

The appendages of the male differ little from those of the female. The antenna has six podomeres but the end claws are very similar to those of the female. The prehensile palps of the first thoracic leg are dissimilar and unequal, the left (fig. 47b) being longer than the right (fig. 47a). Both are slightly curved distally and each has a distal seta and a medial one. The medial one is located more than one-third of the distance from the distal end of the left palp, less than one-third of the distance in the right palp. The penis (fig. 48) is widened distally and the outer lobe is unequally bilobed (fig. 48-O).

*Remarks:* Although the shell in this species is slightly higher than one-half of the length, there can be little doubt that it is distinctly a member of the Acuminata group. This species not only possesses the characters recognized as belonging to members of the group Acuminata but it also bears a close resemblance to some of the European members assigned to the Acuminata group. The posterior margin of the shell is oblique or truncate and shows a posterior-ventral angle similar to *C. levanderi* Hirschmann 1912 (Hirschmann, 1912), and *C. lapponica*

Ekman 1908 (Sars, 1928) from Europe. In size *C. indigena* is larger than *C. lapponica* but a little smaller than *C. levanderi*.

*Ecology:* *Candona indigena* is an inhabitant of temporary ponds where it seems to be well adapted to living in masses of decaying leaves and vegetation on otherwise more or less bare bottom in rather shallow water. As this species is distinctly an inhabitant of temporary ponds and sloughs, it is taken only during the vernal season.

*Distribution:* This species has been taken in three collections from east central Illinois: two collections from Seymour Prairie, Champaign County, on April 15, 1940, and one from Busey's Pasture, Urbana, Champaign County, on the same date. Two individuals were collected near Congerville, Woodford County, on May 28, 1940, and a few individuals of this species were found in a collection made by Robert Yapp from a slough near Reelfoot Lake, Tennessee, on March 22, 1940.

The holotype (female) and allotype (male) of this species are deposited in the U. S. National Museum (Cat. Nos. 81070 and 81071). Paratypes are in the collections of Dr. H. J. Van Cleave, Dr. Arthur G. Humes, and the writer.

*Candona suburbana* sp. nov.

(Pl. IV, figs. 49-54; pl. V, figs. 55-57)

(?) *Candona elongata* Herrick 1879 sp. indet. Herrick, 1879:113, pl. 20, figs. 2, 2a, b, c.

*Type Locality:* Busey's Pasture, Urbana, Champaign County, Illinois.

*Description of the Female:* A *Candona* species belonging to the *Acuminata* group. The shell (fig. 49) of the single female (allotype) examined is elongated, over twice as long as high. After mounting in diaphane, the right valve measures 1.04 mm. in length and 0.47 mm. in height; the left valve, being considerably larger, measures 1.08 mm. in length and 0.51 mm. in height. The width is about four-fifths of the height. The ventral margin has a sinuation in the posterior part of the anterior one-half of the shell; the anterior end is slightly more evenly and broadly rounded than the posterior end. In the left valve, the dorsal margin is nearly evenly rounded, passing more or less insensibly into the anterior and posterior margins although a very slight sinuation is indicated in the dorsal margin and between the dorsal and anterior margins. In the right valve, on the other hand, the sinuation of the dorsal margin and those between the dorsal and anterior and dorsal and posterior margins are more evident.

The surface of the shell bears a considerable number of short, weak hairs each of which is set on a well marked papilla. The hairs of the anterior and posterior margins are few in number and are weakly de-

veloped. Pore-canals are conspicuous at both ends as well as along the ventral margin. The muscle scars are somewhat anterior of the center of the shell and are very definite in arrangement. There are five scars forming a rosette with a single isolated one above the group and two isolated scars slightly anterior-ventral to the rosette.

The distal five podomeres of the antennules become regularly longer and narrower distally; the fifth and sixth podomeres have an outer seta longer than the length of the next podomere; the fifth, sixth, and seventh podomeres each has two long medial swimming setae. Distally, the eighth podomere bears two setae longer than one and one-half times the length of the podomere, one seta about half again as long as the short ones, and a very long swimming seta. The antennae have a group of four setae on the distal one-third of the penultimate podomere; the longest distal claw extends but little if any beyond the longest claw of the penultimate podomere. The medial distal seta of the penultimate podomere of the mandibular palp is smooth; there are four setae in the group on the antepenultimate podomere. The mandibular teeth consist of five very heavy teeth and two or three small, rudimentary teeth. Of the twenty-two rays in the branchial plate of the maxilla, four are directed orally.

The second leg (fig. 52) has the second podomere almost equal in length to the sum of the lengths of the third and fourth podomeres. The second podomere bears a distal seta shorter than the distal width of the podomere. The third and fourth podomeres are approximate in length with the distal seta of each, about equal in length to the length of the ultimate podomere of the appendage. The ultimate podomere is nearly twice as long as wide and bears distally a short seta about equal in length to the podomere, another three-fourths as long, and a claw slightly subequal in length to the sum of the lengths of the distal three podomeres of the appendage. The third thoracic leg appears to be formed of five podomeres through the division of the penultimate. The basal podomere bears two seta. The apparent second and third podomeres seem to bear no setae; the seta of the penultimate podomere is longer than the length of the podomere. The ultimate podomere is nearly square. The length of the shortest distal seta is four times the length of the ultimate podomere and is about one-half the length of the longer companion seta. The oppositely directed seta has a length about two times that of the shorter seta of the pair.

The furcal rami are nearly straight. The length of the ventral margin of the ramus is about eleven times the least width; the length of the dorsal seta is three and one-half to nearly four times the least width of the ramus and is located about one-third of the length of the dorsal margin from the distal end of the ramus. The finely toothed terminal

claw is about one-half as long as the ramus. The length of the terminal seta is about one and one-half times the least width of the ramus. The genital lobe (fig. 54-G) is moderately well developed, being triangular and lacking the long finger-like projection often seen in members of the *Acuminata* group. The genital lobes do not extend beyond the dorsal margin of the furcal rami.

*Description of the Male:* The shell (fig. 50) of the male is slightly larger than that of the female. Measurements of valves mounted in diaphane are as follows:

RIGHT		LEFT	
Length	Height	Length	Height
1.00 mm.	0.— mm.	1.12 mm.	0.56 mm. (holotype)
1.13	0.55	1.16	0.58
1.12	0.52	1.16	0.54

The ventral margin is much more deeply sinuated than in the female shell. The dorsal margin, as a rule, is regularly and evenly arched and passes insensibly into the anterior and posterior margins. There are no evidences of sinuations in the center or at the ends of the dorsal margin except a slight dorsal flattening, which occurs in a few valves. A dorsal view (fig. 51) of the shell shows the sides to be rather evenly rounded and the ends somewhat pointed, the anterior more so than the posterior.

The antennules, mandibles, and maxillae are similar to those of the female. The antennae are slightly different in having lost the group of four setae on the penultimate podomere and in having acquired the customary heavy male seta at the distal end of the antepenultimate podomere. The second thoracic leg of the male differs from that observed in the female as follows: the second podomere is almost equal in length to the sum of the lengths of the three distal podomeres, the third podomere is slightly longer than the fourth, the seta of the third podomere is a little longer than in the female, and the terminal claw is slightly longer in relation to the length of the ultimate podomere. As the description of the female is based upon a single specimen, it is difficult to determine whether or not the slight differences between male and female appendages are the result of individual variation or are sexual differences. The third thoracic leg of the male (fig. 53) is essentially like that of the female.

The furca (fig. 55) of the male is more slender than the furca of the female and somewhat curved so that the ventral or anterior margin is slightly convex. The length of the ventral margin is nearly fourteen times the least width of the furcal ramus. The dorsal seta is located one-third of the length of the dorsal margin from the distal end of the furca.

The length of the dorsal seta is over four times the least width of the ramus, being about one-half as long as the terminal claw which, in turn, is about one-half as long as the ventral margin of the furcal ramus. The length of the terminal seta is twice the least width of the ramus. There is a very slight tendency in some instances to have an S-curvature in the terminal claw and more especially in the subterminal claw. This curvature is not pronounced.

The prehensile palps are unequal and somewhat similar; the right (fig. 56b) being rather large and stout, the left (fig. 56a) smaller and with a widening at the distal end. The penis (fig. 57) is oval in general outline, with prominent outer lobe (fig. 57-O).

*Remarks:* Because of the number of both American and European species belonging to the group *Acuminata*, it is difficult to establish a definite relationship between *C. suburbana* sp. nov. and other described species. Four species described by Furtos (1933) seem to be related to *C. suburbana*, at least superficially. However, it is impossible to ascertain from the descriptions given by Furtos that her species belong to the group *Acuminata* because that writer fails to give many of the characteristics necessary for assignment of particular species to the proper group. These possibly related species and the ways in which they differ from *C. suburbana* are as follows: (1) *C. suburbana* differs from *C. eriensis* Furtos 1933 in the undivided penultimate podomere of the third leg of the latter; the penis is wider; the shell has a conspicuous posterior-dorsal angulation and shows only six muscle scars. (2) *C. suburbana* differs from *C. scopulosa* Furtos 1933 in shell shape and in the unclear division of the penultimate podomere of the third thoracic leg in the latter form. The female genital lobe is much longer, the prehensile palps more curved, and the penis wider in *C. scopulosa*. (3) *C. decora* Furtos 1933 differs from *C. suburbana* in having the shell larger with a well angulated dorso-posterior margin. *C. decora* also has a much longer female genital lobe. (4) *C. distincta* Furtos 1933 differs from the new species by a well marked angulation and sinuation near the point where the posterior and dorsal margins of the shell meet. In a view from above, the fairly well rounded ends of the shell of *C. distincta* are in contradiction to the more pointed ends of *C. suburbana*. Other differences also occur. *C. suburbana* is also related to several species of *Candona* from Illinois. A comparison of these species with *C. suburbana* is given under the "remarks" in the description of *C. acuta* and needs not be repeated.

It is possible that *C. suburbana* may be the *C. elongata* described by Herrick (1879). Herrick's description is so incomplete and his figures so poor that it is impossible to make out with certainty just what species he actually collected. G. W. Müller (1912) through a gross error thought

that *C. caudata* Kaufmann 1900 was a synonym of *C. elongata* Herrick 1879 and took the name given by Herrick to be the valid name. Since then, Klie (1938a) and others have realized Müller's mistake and have rejected the name *C. elongata* Herrick. It is very obvious that *C. elongata* Herrick is not the same ostracod as *C. caudata* Kaufmann, as may be readily seen in a comparison of the shell of the two forms. While there is a remote possibility that *C. suburbana* and *C. elongata* might be the same, it is impossible to determine this with certainty on the basis of Herrick's inadequate description. In Herrick's figures (pl. 20, figs. 2, 2a, b, c) the shape of the shell, form of the antennae, and form of the prehensile palps indicate a *Candona*, but, at the same time, some of the setae are lacking from the third thoracic leg, the antennules have too few podomeres, and the ejaculatory duct is too much shortened for a *Candona*. If Herrick, who stated that he did not know whether the species is a *Candona* or a *Cypris* species, could not properly place the species in the genus and could not give figures which would make possible definite determination of the genus, certainly it is not safe to use his specific determination. To the present writer, it seems inadvisable to accept Herrick's name in view of the fact that his description and figures are so inadequate. If the type locality of *C. elongata* Herrick were known, it might be possible to secure topotypes and clear the situation, but the type locality is nowhere mentioned by Herrick.

*Ecology:* *C. suburbana* sp. nov. was taken from a temporary pond (ox-bow) which usually dries up at least by the serotinal season. The collections were made by dragging a plankton net in the grass along the edge of the pond where the water was from three to six inches deep. The water was clear and some algae were present.

*Distribution:* The writer has taken *C. suburbana* in only two collections from pond No. 2, Busey's Pasture, on the north outskirts of Urbana, Illinois. On May 22, 1940, eight mature males were taken and on June 9, 1940, a single mature female was obtained. Several previous and later collections from the same pond contained no individuals of this species.

The holotype (male) and the allotype (female) are deposited in the U. S. National Museum (Cat. Nos. 81073 and 81072). Paratypes (male) are in the collections of Dr. H. J. Van Cleave and the writer.

*Candona fossulensis* sp. nov.

(Pl. V, figs. 58-64)

*Type Locality:* Champaign County, Illinois.

*Description of the female:* A *Candona* of the *Acuminata* group. The shell has a height of more than one-half the length and is highest near the beginning of the posterior third. The left valve (fig. 58) has a slightly

convex dorsal margin with a weak sinuation at the junction of the dorsal and anterior margins. The anterior end is evenly and narrowly rounded. The posterior end is broadly rounded, appearing subtruncate and having the union of the dorsal and posterior margins marked by an angulation. The ventral margin is flatly concave with the concavity deepest near the center of the margin. The right valve is very similar in shape to the left with the exception that the sinuation between the dorsal and anterior margins is much more pronounced. The left valve is slightly larger than the right. The width of the shell is considerably less than the height. Measurements of the length and height of valves mounted in diaphane are as follows:

RIGHT		LEFT	
<i>Length</i>	<i>Height</i>	<i>Length</i>	<i>Height</i>
0.99 mm.	0.52 mm.	1.00 mm.	0.54 mm. (holotype)
1.00	0.52	1.02	0.54
1.04	0.55	1.06	0.57

The shell margins exhibit many fine hairs especially at the anterior and posterior ends. Because of the proximity of the submarginal line and the valve margin, the pore-canals are obliterated except along the ventral margin in an area just anterior to the ventral sinuation. There is a rosette of five muscle scars with a single scar just above the rosette. This rosette is placed anterior to the center of the valve. A short distance ventral and anterior are two additional small, well-separated scars and some distance anterior and dorsal of the group are two more very small isolated scars. Posteriorly the shell has very peculiar markings (fig. 59) which divide the surface of the shell into irregular square and diamond-shaped areas. This sculpturing is conspicuous anterior to the posterior margin in an area which might be called the posterior slope. The markings cannot be observed in the anterior four-fifths of the shell.

The antennules and antennae are slender with the swimming setae of the former and the claws of the latter long and slender. The distal podomere of the antennules is nearly six times as long as wide; the fourth podomere is about as long as wide, and the more distal ones are all cylindrical. The terminal claws of the antennae reach to the level of the tips of the longest claws of the penultimate podomere. The penultimate podomere is well over twice as long as wide. The length of the sensory bristle of the antepenultimate podomere is less than the width of the podomere. The two distal podomeres of each mandibular palp (fig. 60) are more slender than in many Candona; the medial distal seta of the penultimate podomere is smooth, and the bundle on the antepenultimate podomere consists of four setae (fig. 60-S). The two terminal claws of the mandibular palp are short and heavy.

The second thoracic leg has the second podomere nearly equal in length to the sum of the lengths of the three distal podomeres and equal

in length to the distal claw of the appendage. The apparent penultimate and antepenultimate podomeres are equal in length; the length of the ultimate podomere is approximate to one-half the length of the penultimate. The ultimate podomere is longer than wide. The seta of the penultimate podomere is approximately three-fourths as long as the length of the podomere; the seta of the antepenultimate podomere is equal to the seta of the penultimate while the seta of the second podomere is usually slightly shorter. Considerable variation occurs in the relative lengths of the setae of the second leg. The basal podomere of the third thoracic leg (fig. 61) bears two setae. The penultimate podomere is divided; the ultimate podomere is as wide as long. The shortest distal seta is four times as long as the width of the ultimate podomere; the companion seta is a little less, and the oppositely directed seta a little more, than twice as long as the shortest distal seta.

The furca (fig. 62) is gently curved; the length of the ventral margin is nine times the least width of the ramus. The dorsal seta has a length equal to three or three and one-half or in some individuals nearly four times the least width of the furcal ramus. The dorsal seta is located a distance from the subterminal claw usually equal to a little more than three times the least width of the furca. The length of the terminal claw is a little less than one-half the dorsal margin of the furcal ramus. The length of the terminal seta is equal to the least width of the furcal ramus. The genital lobe (fig. 62) consists of a long finger-like projection attached to the dorsal-posterior margin of a large hemispherical base. The finger-like lobe has a concave, sometimes almost straight but never convex, dorsal edge and a convex ventral edge. The lobe is often distally bent dorsad.

*Description of the Male:* The shell of the male is similar to that of the female but slightly larger. The ventral sinuation of the shell of the male is more pronounced and somewhat anterior to the center of the ventral margin. Measurements of the valves of three males are as follows (mounted in diaphane):

RIGHT		LEFT	
Length	Height	Length	Height
1.12 mm.	0.60 mm.	1.13 mm.	0.61 mm. (allotype)
1.18	0.62	1.20	0.64
1.17	0.59	1.19	0.—

The cephalic and thoracic appendages of the male resemble those of the female with the exception that the second thoracic legs are more slender.

The furca of the male is more slender than that of the female; the length of the ventral margin is from twelve to thirteen times the least width. Because of the slender condition of the distal end of the furcal

ramus, the dorsal seta has a length over four times the least width of the ramus and the length of the terminal seta is one and one-half times the least width of the ramus. The terminal claw has a length equal to about two-fifths of the dorsal margin of the ramus. The prehensile palps are dissimilar and somewhat unequal. The right (fig. 63a) is heavy and falciform; the left (fig. 63b) is less stout, and the tip extends straight without change in diameter for some distance distal of the bend of the palp. The penis (fig. 64) is wide and rather short; the middle and inner lobes are not well developed and do not extend beyond the penis proper; the outer lobe appears as a lappet with what appears to be a tubule ending at the margin a short distance dorsal to the tip of the lobe.

*Remarks:* Of all the described species of *Candona*, *C. decora* Furtos 1933 seems to be the most closely related to *C. fossulensis* sp. nov. That the two species are related is shown by the agreement of the two species in general shell shape and sculpturing and in the similarity of the penis and prehensile claws. The characteristics in which *C. fossulensis* sp. nov. and *C. decora* Furtos differ may be listed as follows:

	<i>C. decora</i> Furtos 1933	<i>C. fossulensis</i> sp. nov.
Female, size of shell.....	1.18-1.30 x 0.63-0.70	1.00-1.05 x 0.54-0.57
Male, size of shell.....	1.4-1.5 x 0.7-0.8	1.12-1.2 x 0.60-0.64
Dorsal-posterior angulation.....	More	Less
Female: 3rd leg, last podomere.....	Length more than width	Length equals width
Short seta, 3rd leg.....	3½ x last podomere	4 x last podomere
Furca, ventral margin.....	13 x least width	9 x least width
Furca, dorsal seta.....	¾ of subterminal claw	¾ or ¾ of sub-terminal claw
Furca, dorsal seta.....	¾ from distal end of ramus	¾ from distal end of ramus

A comparison of the characters of *C. fossulensis* with related *Acuminata* species from Illinois is given under *C. acuta* described herein.

*Ecology:* The type specimens were taken from a roadside ditch in which the water was three inches deep and the bottom was covered with dead grass. Another collection was made on the same date in a nearby vernal pond in which the water was up to twelve inches deep and there was little dead grass on the bottom.

*Distribution:* *C. fossulensis* sp. nov. has been taken in only two collections. These were from separate bodies of water in the same vicinity near Seymour, Champaign County, Illinois. The two collections were made on April 1, 1940.

The holotype (female) and allotype (male) of *C. fossulensis* are deposited in the U. S. National Museum (Cat. Nos. 81068 and 81069). Paratypes (female and male) are in the collections of Dr. H. J. Van Cleave, Dr. Arthur G. Humes, and the writer.

*Candona acuta* sp. nov.

(Pl. V, figs. 65-69; pl. VI, figs. 70-72)

*Type Locality:* Illinois.

*Description of the Female:* A *Candona* of the *Acuminata* group with the shell height and width approximating one-half of the shell length. The dorsal margin is flatly arched (fig. 65); the anterior end is narrowly and evenly rounded, a definite sinuation separating anterior and dorsal margins. The ventral margin has a very conspicuous sinuation slightly anterior to the mid-point, with the margin between the sinuation and the posterior-ventral angulation flattened. The posterior end has a bluntly rounded, subtruncate margin. The posterior and ventral margins join at nearly a right angle in the right valve. There is a very slight sinuation between the dorsal and posterior margins but this is more apparent than real as it is caused largely by the extension of the valve beyond the posterior shell margin. The ovary appears as a narrow band, posteriorly much more narrowed than in most *Candona*. The muscle scars consistently occur in a greater number than in many *Candona* as there is a nearly centrally located rosette of five loosely arranged scars, a single scar slightly more dorsad, two scars some distance anterior-ventrad, and two smaller scars anterior-dorsad of the rosette. The submarginal line is close to the margin of the valves so that the pore-canals are very short. The surface of the shell bears a few scattered hairs which are fairly conspicuous along the margins. From below (fig. 66), the sides of the shell form an even arc with the anterior slightly more pointed than the posterior.

The right valve of the holotype measures 1.07 mm. in length, 0.54 mm. in height, and 0.56 mm. in width. Measurements of the valves of other mature females (paratypes) are as follows (mounted in diaphane):

RIGHT		LEFT	
<i>Length</i>	<i>Height</i>	<i>Length</i>	<i>Height</i>
1.06 mm.	0.53 mm.	1.10 mm.	0.56 mm.
1.05	0.54	1.09	0.56
1.08	0.55	1.13	0.58

The antennules show few characteristics helpful in specific diagnosis. The fifth, seventh, and eighth podomeres are equal in length; the sixth is slightly shorter. The antennae are short and stout; the terminal claws are very heavy and not proportionally as long as in many *Candona*. The longest claw of the penultimate podomere extends beyond the longest claw of the ultimate podomere. The penultimate podomere bears submedially a group of four small setae near the distal end of the podomere. The sensory organ of the antepenultimate podomere is much reduced, being

little more than one-half as long as the width of the podomere at the same level.

The medial-distal seta of the penultimate podomere of the mandibular palp is smooth; the bundle of setae on the antepenultimate podomere contains four setae. The second thoracic leg (fig. 67) has the length of the second podomere equal to the sum of the lengths of the distal three podomeres. The penultimate (fig. 67-P) is hardly as long as the antepenultimate podomere; the seta of the antepenultimate podomere reaches to the base of the seta of the penultimate and is not as long as the seta of the penultimate. The ultimate podomere is longer than wide and, besides the claw, bears a distal seta longer than the podomere and a sub-distal seta equal to the length of the podomere. The terminal claw is usually a little longer than the sum of the lengths of the last three podomeres and is commonly recurved toward the distal end. The sides of the second, third, and fourth podomeres bear small spines.

The third thoracic leg (fig. 68) consists of five apparent podomeres through the division of the penultimate podomere (fig. 68-P). The basal podomere has two setae, both of which are long. The seta of the penultimate podomere is sometimes bent near the distal end and is very long; being approximate to the short seta of the ultimate podomere, it has a length equal to the sum of the length of the apparent antepenultimate and penultimate podomeres. There are a few very short spines along the sides of the penultimate podomere. The ultimate podomere is little longer than wide. The shortest of the three distal setae is nearly four times the length of the ultimate podomere; the companion seta is about twice as long as the shorter; the length of the oppositely directed seta is variable, either sub-equal or equal to the longer one of the pair and, like the shortest distal seta, is distinctly bent near the distal end.

The furcal ramus (fig. 69-R) is somewhat curved; the length of the ventral margin is ten times the least width. The dorsal seta (fig. 69-D) has a length of two and one-half times the least width of the ramus and is removed from the subterminal claw by a distance equal to a little less than one-third of the ventral margin. The length of the terminal seta is one and one-fourth times the least width of the furcal ramus. The claws are gently curved throughout their length; the length of the terminal claw is approximate to one-half of the length of the ventral margin of the furcal ramus. The claws are very finely toothed. The female genital lobe (fig. 69-G) is well developed, bluntly pointed at the posterior end, and separated from the thorax by a slight constriction. There is a seta (fig. 69-B) on the dorsal portion of the thorax near the base of the furca.

*Description of the Male:* The shell (fig. 70) of the male differs considerably from that of the female. The posterior end is broadly rounded,

COMPARISON OF SOME CLOSELY RELATED SPECIES OF THE ACUMINATA GROUP AS FOUND IN ILLINOIS

	<i>C. caudata</i> Kaufmann 1900	<i>C. sigmoides</i> Sharpe 1897	<i>C. indigena</i> <i>sp. nov.</i>	<i>C. subarbana</i> <i>sp. nov.</i>	<i>C. fossulensis</i> <i>sp. nov.</i>	<i>C. acuta</i> <i>sp. nov.</i>
Shell length	1.15-1.35 mm.	1.06 mm.	0.95-1.10 mm.	1.08 mm.*	1.00-1.06 mm.	1.10-1.13 mm.
Shell height	0.50-0.65 mm.	0.55 mm.	0.55-0.65 mm.	0.51 mm.*	0.54-0.57 mm.	0.56-0.58 mm.
Junction of posterior and ventral margins	Angulation in left valve	Angulation in left valve	Wide angle	Rounded	Rounded	Angulation in right valve
Length of distal claw of second leg	Equals distal three podomeres	Equals distal three podomeres	Equals $1\frac{1}{4}$ times distal three podomeres	Less than sum of distal three podomeres	Nearly equals sum of distal three podomeres	Equals distal three podomeres
Furca:— Length of ventral margin	11 times least width of ramus	$9\frac{1}{2}$ times least width of ramus	9 times least width of ramus	11 times least width of ramus	9 times least width of ramus	9-10 times least width of ramus
Length of dorsal seta	2 times least width of ramus	$3\frac{1}{4}$ times least width of ramus	$3\frac{1}{2}$ times least width of ramus	$3\frac{1}{4}$ times least width of ramus	$3\frac{3}{4}$ times least width of ramus	$2\frac{1}{2}$ times least width of ramus
Length of terminal seta	Same as least width of ramus	$1\frac{1}{4}$ times least width of ramus	$1\frac{1}{2}$ times least width of ramus	$1\frac{1}{2}$ times least width of ramus	Same as least width of ramus	$1\frac{1}{4}$ times least width of ramus
Female genital lobe	Moderately long cone	Finger-like	Narrow, finger-like	Triangular	Hemispherical base; long projection	Separated from thorax by a constriction

\*Measurements based on a single individual.

the anterior narrowly rounded. The dorsal margin is relatively uninterrupted and passes as an arc from the posterior to the anterior margins. The ventral margin is deeply sinuated, the sinuation being followed posteriorly by a flattened area along the ventral margin. In some shells, there is a slight angulation at the juncture of the posterior and dorsal margins and a slight sinuation at the beginning of the anterior margin. Measurements of the valves of several males (mounted in diaphane) are as follows:

RIGHT		LEFT	
Length	Height	Length	Height
1.24 mm.	0.62 mm.	1.28 mm.	0.64 mm. (allotype)
1.19	0.59	1.22	0.62
1.26	0.64	1.31	0.69

The antennules and antennae are essentially like those of the female except for the presence of the male setae and the loss of the group of four small setae already mentioned. The second thoracic leg is like that of the female except in some males the entire appendage has a tendency to be slightly more slender with the terminal claw proportionally longer and often not recurved near the distal end. The third thoracic leg is similar to that of the female. In the furca, the ramus between the base of the dorsal seta and the subterminal claw is very narrow. This results in the length of the ventral margin being about fifteen times the least width of the ramus. The narrowed portion of the ramus is strongly curved. As a result of the narrowness of the furca, the dorsal seta has a length of about four and one-half times the least width and the terminal seta is nearly twice as long as the ramus is wide.

The prehensile palps are unequal and dissimilar. The left (fig. 71a) has a very long, straight, and narrowed distal portion; the right (fig. 71b) is falciform, shorter, and stouter than the left. Considerable variation is shown in the prehensile palps, especially in the left where the degree of relative narrowness and length is often different from that shown in the pictured paratype. The penis (fig. 72) is elongated, the outer lobe (fig. 72-O) well developed and the other two lobes small and poorly developed.

*Remarks:* A tabular comparison of *C. acuta* with closely related species of the Acuminata group as found in Illinois is given herewith. (The chart compares females only.)

*Ecology:* Most collections of *C. acuta* sp. nov. have been made in grass and decaying vegetation along the edges of small streams, usually temporary, three to eight feet wide, and up to two feet deep, where the water is clear and cool and there is considerable current. In one instance, the species was taken from a pond connected to a small stream only during high water stages and, in another instance, from the stomach of a fish,

*Catostomus commersonii*, from the stripland ponds near Oakwood, Illinois. The species seems not to be restricted to any season, having been taken in May, July, and November.

*Distribution:* *C. acuta* *sp. nov.* has been taken from Champaign County, Livingston County, and Vermilion County, Illinois. The species seems to be restricted to the cooler waters of the state and has not been collected from the southern part of the state. It has not been reported outside of Illinois.

The holotype (female), allotype (male), and two paratypes (one female, one male) are deposited in the U. S. National Museum (Cat. Nos. 81074, 81075, 81076, and 81077). Other paratypes (both female and male) are in the collections of Dr. H. J. Van Cleave, Dr. Arthur G. Humes, and the writer.

#### *Group Fabaeformis*

The group of setae on the antepenultimate podomere of the mandibular palp consists of three or five setae. Characters otherwise as in the group *Acuminata*.

Upon the basis of present information, it is impossible to assign any Illinois species definitely to the group *Fabaeformis*. *C. sharpei* *sp. nov.* may belong here, especially as this species was formerly assigned to the European species *C. fabaeformis* Fischer 1851 by Sharpe (1897, 1918). However, the inadequate available description seems to point to the placement of this species in the group *Acuminata*. As a result, *C. sharpei* *sp. nov.* has been tentatively assigned to the group *Acuminata* but may be reassigned when more details of its structure become known.

### SUBFAMILY CYCLOCYPRINAE

Shell usually short and high, more or less rounded (figs. 76, 98). Swimming setae of the antennae well developed (fig. 76-A) but occasionally reduced; usually twice as long as the distance from their origin to the tips of the terminal claws of the antennae. Antenna in female of five, in male of six podomeres through a division of the penultimate podomere. The first thoracic leg with well developed respiratory plate; the palp (endopodite) in the female consists of one or two podomeres; in the male it is modified as a grasping palp or prehensile palp of two podomeres (fig. 80). The distal podomere of each palp forms a movable finger called the dactylus (fig. 80a-D) and rests on the proximal podomere which is designated as the propodus (fig. 80b-P). Third thoracic leg with three distal setae (figs. 84, 91), of which one is long and reflexed, the other two are much shorter and not reflexed in most species. Ductus

ejaculatorius (fig. 93) with the proximal extremity of the tubule forming a dilated pouch, the distal end forming a funnel-shaped sac leading into the vas deferens.

The subfamily Cyclocyprinae replaces as a taxonomic unit the subfamily Cyclocypridinae used by Sharpe (1903, 1918). Many writers, as Furtos (1933), prefer to group the genera belonging to the Candoninae and Cyclocyprinae into the subfamily Candocyprinae, which is then subdivided into *tribes* of less than subfamily and more than generic importance. The tribe Cyclocyprini is used by Furtos (1933, 1935) as an equivalent to the subfamily Cyclocyprinae as used herein. To the present writer, it seems desirable to avoid the use of such subdivisions as tribes which tend to complicate the system of classification without introducing any real advantage not gained by a simpler system.

As found in Illinois, the subfamily Cyclocyprinae includes three genera: Cyclocypris Brady and Norman 1889, Cypria Zenker 1854, and Physocypris Vávra 1897. A fourth American genus, Candocypris Furtos 1933, is found in Ohio but has not been discovered in Illinois.

#### KEY TO GENERA OF THE SUBFAMILY CYCLOCYPRINAE IN ILLINOIS

- 1a. Shell tumid; the last podomere of the third thoracic leg at least twice as long as wide (fig. 75).....Genus CYCLOCYPRIS Brady and Norman 1889
- b. Shell compressed; the last podomere of the third thoracic leg not much longer than wide (figs. 84, 89).....2
- 2a. Valves nearly equal, margin of both valves smooth (fig. 76).....Genus CYPRIA Zenker 1854
- b. Valves commonly unequal in height or length or both; margin of either right or left valve more or less tuberculated (fig. 98).....Genus PHYSOCYPRIS Vávra 1897

#### GENUS CYCLOCYPRIS BRADY AND NORMAN 1889

Shell rounded, height and width greater than one-half the length (fig. 73); surface of shell smooth, brown in color. Eye well developed. Swimming setae of both antennules and antennae are long and well adapted for swimming. The penultimate podomere of the second antenna in the male is divided, but no specialized male setae are present. Respiratory plate of the first thoracic leg with six plumose setae. Third thoracic leg consisting of four podomeres (fig. 75); the ultimate podomere elongated, more than twice as long as wide and usually at least one-half as long as the penultimate podomere. Ultimate podomere of third leg with three distal setae, unequal, with the outermost one very long and reflexed. The dorsal setae of the furca often greatly reduced and usually removed some distance from the subterminal claw.

KEY TO SPECIES OF THE GENUS *CYCLOCYPRIS* IN ILLINOIS

- 1a. Shell less than 0.5 mm. in length; terminal seta of the furca at least three-fourths as long as the terminal claw; dorsal seta of furcal ramus absent or rudimentary.....*C. sharpei* Furtos 1933
- b. Shell over 0.5 mm. in length; terminal seta of furca not over one-half as long as the terminal claw; dorsal seta of furcal ramus present.....*C. forbesi* Sharpe 1897

*Cyclocypris forbesi* Sharpe 1897

(Pl. VI, figs. 73-75)

*Cyclocypris forbesi* Sharpe 1897. Sharpe, 1897:432-433, pl. 41, figs. 1-7; 1918:822, figs. 1290a, b, c, d, e, f; Furtos, 1935:535-537, fig. 3.

*Type Locality:* McLean County, Illinois.

*Description of the Female:* An ostracod of the genus *Cyclocypris*. According to Sharpe (1897), the shell measures 0.55 mm. in length, 0.39 mm. in height, and 0.36 mm. in width. The single female individual observed in the present writer's collection was slightly larger, measuring 0.62 mm. in length and 0.47 mm. in height. The shell (fig. 73) is plump with the right valve slightly larger than the left. The height is almost equal to three-fourths of the length. The color of the shell is a sepia brown and there are occasional hairs especially along the margins. The shell is subelliptical with the dorsal margin arched. The posterior margin is more broadly rounded than the anterior margin.

The ultimate podomere of the antenna is about as long as wide, the penultimate is about four times as long as the ultimate, and the antepenultimate is more than one and one-half the length of the penultimate. The sensory organ of the antepenultimate podomere is extremely long, reaching past the distal end of the podomere to which it is attached. The terminal claws are curved near the tip, beyond which the swimming setae reach a distance equal to three times the length of the terminal claws.

The curved terminal claw of the second thoracic leg (fig. 74) has a length equal to more than the sum of the distal three podomeres of the leg. The third thoracic leg (fig. 75) has the "terminal segment . . . three fifths as long as the preceding segment. The longer of the backwardly directed setae is longer than the combined lengths of the last three segments, the shorter one being one fourth as long, or the length of the last segment; terminal claw half as long as the last segment" (Sharpe, 1897). The furca is somewhat bent, the terminal claw is about one-half as long as the ventral margin of the ramus, and the subterminal claw is four-fifths as long as the terminal. Both claws are strongly bent at the tip. "Terminal seta about as long as width of the ramus; dorsal seta delicate, two and a half times width of ramus from subterminal claw, and two thirds as long as ramus is wide" (Sharpe, 1897).

*Description of the Male:* The male is very adequately described by Furtos (1935). It is much the same in general shape and size as the female. The prehensile palps are unequal and elongated; "ejaculatory duct quite small, with crowns of spines surrounding openings easily visible, the others quite obscure. Penis roughly quadrangular with a beak-like terminal lobe" (Furtos, 1935). The male was not observed by the present writer.

*Remarks:* Sharpe seems to have made a mistake in regard to the setae of the penultimate podomere of the third thoracic leg when he states: "Penultimate podomere three and a half times as long as broad and armed on the inner edge with but one seta, which is on the middle of the segment, and half its length" (Sharpe, 1897). In the individual observed by the present writer there is a seta in the middle and another at the distal end of the podomere as is usual in the genus *Cyclocypris*. Furtos (1935) pictures two setae of nearly equal length on the penultimate podomere. It is entirely possible that Sharpe examined some damaged individuals. The present writer has often found, especially in the *Cyclocyprinae*, that the distal seta of the penultimate podomere of the third thoracic leg may easily become broken.

*Ecology:* The type specimens were collected from a woodland pond near Bloomington, Illinois, on April 5, 1879 (Sharpe, 1897). Furtos (1935) took her material from a pond, details of which are not given. The present writer found a single female in a collection made from mats of vegetation (*Chara*, *Myriophyllum*, and *Potamogeton*) from a lake in northeastern Illinois.

*Distribution:* This species has been reported from McLean County, Illinois, by Sharpe (1897) and from Falmouth, Cape Cod, Massachusetts, by Furtos (1935). The writer has it in a single collection from Illinois. This collection, made by Mr. Bert Wright, was from East Loon Lake, near Antioch, Lake County, Illinois, on August 7, 1940.

#### *Cyclocypris sharpei* Furtos 1933

*Cyclocypris laevis* Sharpe 1908 (non O. F. Müller 1785). Sharpe, 1908:408-410, pl. 50, fig. 5, pl. 54, figs. 5-7.

*Cyclocypris laevis* Sharpe 1918 (non O. F. Müller 1785). Sharpe, 1918:822, fig. 1289a, b, c.

*Cyclocypris sharpei* Furtos 1933. Furtos, 1933:460-461, pl. 14, figs. 8-14.

*Type Locality:* Ohio.

*Description of the Female (after Furtos, 1933):* A *Cyclocypris* species measuring 0.47 mm. in length, 0.33 mm. in height, and 0.33 mm. in width. Extremities of shell broadly rounded, posterior somewhat broader; ventral

margin slightly convex. The left valve is the larger. Color chestnut-brown. Ultimate podomere of third leg one-half as long as the penultimate, three times longer than broad. Shortest distal seta one-third as long as the podomere and often S-shaped. Furcal ramus slightly curved; dorsal seta usually absent, sometimes rudimentary; terminal claw one-third as long as the ramus; the terminal seta at least three-fourths the length of the terminal claw.

*Description of the Male (condensed from Furtos, 1933):* Similar to female; length 0.46 mm., height 0.32 mm., breadth 0.32 mm. Prehensile palps short and unequal; penis roughly globose, with one narrow and one broad terminal lobe.

*Remarks:* While it is probable that the true *C. laevis* of O. F. Müller does occur in the United States (Turner, 1895), Sharpe (1908) certainly did not have that species. It seems strange that he did not realize the differences which occur between his form (now called *C. sharpei*) and the true *C. laevis* of O. F. Müller.

*Ecology:* Sharpe (1908) reported this species under the designation *C. laevis* from ponds and swamps southeast of Chicago, Illinois. Furtos (1933) reports *C. sharpei* as being "common in ponds, marshes and lakes." There seems to be no seasonal restriction except that collections so far have not been reported from the haemal season.

*Distribution:* The species was reported from Illinois (southeast of Chicago), Indiana, and New York by Sharpe (1908) and from New Jersey (Sharpe, 1918). Furtos (1933) reports it from several places in Ohio. The present writer has not found individuals of this species in any of his collections from Illinois.

#### GENUS CYPRIA ZENKER 1854

Shell usually short, high (fig. 76), occasionally elongate reniform (fig. 82); strongly compressed; margins smooth, not tuberculate. Eyes well developed. Second antenna of the male with the penultimate podomere divided and bearing specialized male setae. The ultimate podomere of the mandibular palp elongated, often as much as three times as long as the proximal width. Palp of the maxilla well developed, masticatory processes weak. Penultimate podomere of the third thoracic leg undivided (fig. 84); ultimate podomere short (fig. 89), scarcely longer than wide; the longest distal seta is reflexed, the two unreflexed setae equal or unequal and usually not much longer than the length of the ultimate podomere (figs. 84, 89, 91). Terminal and subterminal claws of the furca strong, dorsal seta may be rudimentary (figs. 79, 92). Ductus ejaculatorius with seven whorls of chitinous rays and the proximal end of the duct much inflated (fig. 93). Penis with two terminal lobes only; outer

lobe wanting (fig. 95). In most species, the females are more numerous than the males.

The genus *Cypria* is attributed to Zenker (Zenker, 1854) who used the name "*Cypria*" in a subgeneric sense. However, he gave no diagnosis but described five species in the subgenus. The first available description of the genus *Cypria* appears to be that given by Brady and Norman (1889). In order to place *C. mediana* sp. nov. in the genus *Cypria*, it has been necessary to revert to the original diagnosis of Brady and Norman (1889) rather than the descriptions of later writers who have restricted the genus in various ways. The principal difficulty in fitting *C. mediana* sp. nov. into the genus *Cypria* as diagnosed by recent authors is the condition of the setae of the third thoracic leg. According to Furtos (1933) the third leg is armed distally "with two short and one long setae, the latter reflexed." Klie (1938a) restricts the genus *Cypria* still more in this respect when he writes "Vorletztes Gl. des Putzfusses ungeteilt, Endgl. kurz, seine lange Borste zurückgekrümmt, die beiden vorwärts gerichteten nicht auffallend verschieden und kaum länger als das zugehörige Glied." In *C. mediana* sp. nov. the shorter of the two unreflexed distal setae of the third leg (fig. 84) has a length equal to one and one-half to two times the length of the ultimate podomere and the longer of the pair is twice the length of the shorter. Brady and Norman (1889) place no restriction upon the relative lengths of the distal setae of the third thoracic leg in the genus *Cypria*.

#### KEY TO SPECIES OF THE GENUS CYPRIA IN ILLINOIS

- 1a. Surface of shell marked with closely set parallel and anastomosing longitudinal lines (fig. 78).....*C. turneri* sp. nov.
- b. Surface of shell not so marked.....2
- 2a. Shell over 0.70 mm. long; length of the shorter terminal seta of the similarly directed pair on the third leg equal to one-half of the longer of the pair (fig. 89).....3
- b. Shell less than 0.70 mm. long; length of the shorter of the pair of similarly directed setae of the third leg more than one-half the length of the longer (fig. 91); color bands, blotches, or patches present on shell.....4
- 3a. The length of the terminal claw of the furca almost as long as the ventral margin of the furca (fig. 85); shell elongate with conspicuous concavity in the ventral margin (fig. 86).....*C. mediana* sp. nov.
- b. The length of the terminal claws of the furca little more than three-fifths of the ventral margin of the ramus; shell suboval with almost straight ventral margin (fig. 88).....*C. obesa* Sharpe 1897
- 4a. Three color blotches; one anterior, one posterior, and one behind the eye (fig. 90); length of dorsal seta of furca about equal to the width of the ramus; subterminal claw of ramus heavily toothed (fig. 92)..*C. maculata* sp. nov.
- b. Small specks of pigment arranged in small patches and scattered over most of the shell surface (fig. 96); dorsal seta of furca has a length about twice the least width of the ramus; claws of the furcal rami lightly toothed.....*C. ophthalmica* (Jurine 1820) Brady and Norman 1889

*Cypria turneri* sp. nov.

(Pl. VI, figs. 76-81)

*Cypria striolata* Herrick 1887 (non Brady 1864, synonym of *C. exsculpta* (S. Fischer 1855)). Herrick, 1887:29, pl. 4, fig. 3.

*Cypria exsculpta* Turner 1894 (non *C. exsculpta* (S. Fischer 1855)). Turner, 1894: 13-14, pl. 7, figs. 2-8; 1895:305, pl. 70, figs. 1-8; pl. 72, fig. 3.

*Cypria exsculpta* Sharpe 1897 (non S. Fischer 1855). Sharpe, 1897:465-466, pl. 47, fig. 4; Kofoid, 1908:258; Shelford, 1913:152; Sharpe, 1918:820, figs. 1283a, b, c, d.

*Cypria elegantula* Furtos 1933 (non Lilljeborg 1853). Furtos, 1933:465-466, pl. 15, figs. 8-14; Dobbin, 1941:237, pl. 9, figs. 13-21, pl. 10, figs. 1-2.

*Type Locality:* Illinois.

*Description of the Female:* An ostracod of the genus *Cypria*. From the side, the shell (fig. 76) is subovate; height equal to a little less than two-thirds of the length; highest in or very near the middle. The dorsal margin is strongly arched with a slight flattening anteriorly above the eye; the anterior and posterior ends are rounded, the anterior end slightly more narrow than the posterior end. The ventral margin is usually, but not always, slightly concave. A thin hyaline border is present in both valves, especially along the anterior and posterior margins. From below (fig. 77), the shell appears compressed; the greatest width is near the center and is slightly less than one-half the length of the shell; the anterior end is pointed and the posterior end is rounded. The left valve is slightly the larger. The surface of the shell is marked with peculiar parallel, frequently anastomosing longitudinal lines (fig. 78) which form a network over the entire surface of both valves. The color of the valves is yellow and there are occasionally some light brown markings varying greatly in intensity and extent. These are usually not as conspicuous, however, as they are in many species of the genus *Cypria*, being light in color and often confined to narrow areas along the anterior and posterior margins of the valves. There are a few scattered hairs along the margins. Measurements of valves of several mature females from Illinois are as follows:

RIGHT		LEFT	
Length	Height	Length	Height
0.54 mm.	0.35 mm.	0.55 mm.	0.35 mm. (holotype)
0.55	0.35	0.56	0.36
0.61	0.38	0.61	0.39
0.56	0.34	0.57	0.35

The length of the sensory organ of the antennae equals in length the width of the podomere to which the organ is attached, the width of the podomere being taken at the level of the base of the sensory organ; the organ reaches to the level of the distal margin of its podomere. Swimming setae of the antennae are variable in length, often reaching beyond

the tips of the terminal claws for a distance about equal to three times the length of the longest terminal claw. The terminal claw of the second thoracic leg has a length equal to the sum of the lengths of the antepenultimate and penultimate podomeres. These two podomeres are equal in length. The terminal podomere of the third thoracic leg has a length equal to about one and one-half times the width; the two distal setae of the pair are slightly unequal, one having a length nearly equal to the length of the podomere, the other slightly longer. The terminal seta of the penultimate podomere of the third thoracic leg is wanting while the lateral seta arises from the basal one-third of the podomere. The penultimate podomere is nearly four times the length of the ultimate podomere. The seta of the antepenultimate podomere reaches scarcely to the base of the lateral seta of the next distal podomere, being much shorter than in many Cypria species.

The furca is curved and stout. The ventral margin is seven to seven and one-half times the least width of the ramus. The size of the furcal ramus as given by Furtos (1933) for *C. elegantula* from Ohio is eleven times the narrowest width. This is evidently an error as the furca which she pictures (her pl. 15, fig. 11) has a length-width ratio compatible to that found by the present writer. The dorsal seta of the furcal ramus has a length equal to nearly two times the least width of the ramus or to about one-half the length of the subterminal claw. The dorsal seta is removed from the subterminal claw by a distance equal to two and one-half times the least width of the ramus or one-third of the dorsal margin. The terminal seta has a length about one and one-half times the least width of the furcal ramus. The terminal claw has a length approximately equal to one-half of the dorsal margin of the ramus and the subterminal claw has a length between four-fifths and five-sixths the length of the terminal one. Both claws are curved and nearly smooth. The few distal teeth are so fine that they cannot be seen in well cleared individuals but may be detected in material mounted in glycerine.

*Description of the Male:* The shell of the male is similar to that of the female but slightly smaller. The allotype measures 0.54 mm. in length and 0.34 mm. in height and is representative of the average size. The furca (fig. 79) has the same proportions as the furca of the female but is more curved. The other appendages are essentially like the corresponding ones of the female. The prehensile palps are dissimilar and unequal. The propodus of the left palp (fig. 80a) is over four times as long as wide and the sides are rather straight and parallel; the dactylus is very slender and falciform, being distally recurved. The propodus of the right palp (fig. 80b) is stouter and shorter than that of the left palp. The peculiar ventral-distal process of the propodus of the right palp is shown

in the figure. The dactylus of the right palp is large and highly curved. It is considerably inflated proximally but tapers to an elongated slender distal portion. The penis (fig. 81) is peculiar, being not exactly as shown by Furtos (1933:pl. 15, fig. 14) for *C. elegantula* of Ohio. In the present writer's material, the penis has two lobes each of which has a slender tip. The inner lobe is proximally widened and flap-like but, unlike the other indigenous Cyclocyprinae, it is suddenly constricted to a narrow, re-curved distal point. The middle lobe reaches nearly to the distal end of the inner lobe. It is slender and gently curved throughout the distal one-half. Usually only a small percentage of the individuals in any collection consists of male animals, the females exceeding the males in abundance.

*Remarks:* Individuals of *C. turneri* sp. nov. have long been assigned to the European species *C. exsculpta* (S. Fischer 1855) Brady and Norman 1889. Furtos (1933) assigned individuals which apparently are *C. turneri* sp. nov. to *C. elegantula* Lilljeborg 1853 although the latter is a synonym of *C. exsculpta* (S. Fischer 1855). Although "elegantula" is an older specific name than "exsculpta," it is invalid because the name "elegantula" was used by S. Fischer in 1851 for individuals now known to belong to the species *C. ophthalmica* (Jurine 1820). Although *C. elegantula* (Fischer 1851) has become a synonym of *C. ophthalmica* (Jurine 1820), *C. elegantula* cannot be used in place of *C. exsculpta* (S. Fischer 1855). *C. exsculpta* (S. Fischer 1855) is then the valid designation of the European species into which many writers have placed individuals belonging to a closely related American species which is described herein as *C. turneri* sp. nov.

The correctness of assigning this American Cypria species, which is characterized by parallel longitudinal lines on the shell, to the European species *C. exsculpta* has been questioned by several writers. G. W. Müller (1912) questioned Turner's identification of the American form and did not even mention the form listed by Sharpe under the European name. Furtos (1933) states "There is a possibility that the Ohio species should not be referred to *elegantula* of Europe." She supported her contention by noting the difference in size of the shell, the difference in the penis, and the "smooth furcal claws" of the European species. Regarding the last item, Furtos was incorrect as the claws of the individuals of *C. exsculpta* of central Europe are toothed according to Kaufmann (1900a) who says that the furca "tragt am Ende zwei schmale, gezähnelte Klauen."

After a study of many complete descriptions of the *Cypria exsculpta* indigenous to Europe and after examining a large series of *C. turneri* from Illinois, the writer has found the following substantial differences

between the true *C. exsculpta* of S. Fischer and the American species now designated as *C. turneri* sp. nov.

	<i>C. exsculpta</i> (S. Fischer)	<i>C. turneri</i> sp. nov.
Shell length, female.....	Over 0.70 mm.	Under 0.65 mm.
Shell height/length ratio.....	Over 70%	Under 65%
Ventral margin of shell.....	Convex	Straight or concave
Third thoracic leg.....	Seta of penultimate podomere near center; ultimate podomere elongated	Same near basal one-third of podomere; ultimate podomere relatively short
Penis.....	Oval; inner lobe not distally recurved hook-like	Elongate; inner lobe hook-like distally
Prehensile palps.....	Propodus of right and left palps equal	Propodus of left palp longer than that of right
Ductus ejaculatorius.....	Oval	Elliptical; elongate

Because there are fixed differences and there appears to be no transition between the European *C. exsculpta* and the American *C. turneri*, they are certainly separate and distinct morphological species. The use of the characteristic longitudinal lines as the main taxonomic criterion for the recognition of the species *C. exsculpta* without checking any of the other structures probably led to the early, easily perpetuated error in designation. The specific name, "turneri," suggested for this new species is in memory of C. H. Turner, one of the outstanding early workers on American Entomostraca.

*Ecology:* *C. turneri* sp. nov. is found only in ponds and lakes, never in running waters except in backwaters of rivers or quiet pools of small, usually vernal streams. It is very abundant in temporary ponds. Under the name *C. exsculpta*, Shelford (1913) reports this species as common in ponds of the Chicago region. Sharpe (1897) writes that this species is common in most "running streams" but the present writer with few exceptions has not found this species in streams. It is often found associated with algae, water plants, and grass but may be found in open water as an occasional constituent of plankton. This species is very abundant from March to late June but is sometimes found in the serotinal and autumnal seasons.

*Distribution:* This species has been reported under the name *C. exsculpta* or *C. exsculpta* from Alabama (Herrick, 1887), from Ohio, Georgia, and Delaware by Turner (1894), from Maine by Procter (1933), and from Illinois by Sharpe (1897), Kofoid (1908), and Shelford (1913). The *Cypria exsculpta* mentioned by Creaser (1931) as occurring in crayfish burrows in Missouri is probably also this species. Under *C. elegantula*, this species has been reported from Ohio by Furtos

(1933) and from Washington and Alaska by Dobbin (1941). Since it has been long confused with the European species *C. exsculpta* (S. Fischer 1855), it is impossible to determine its range. *C. turneri* sp. nov. is probably confined, however, to the Nearctic region. The present writer has taken it in collections from counties in many parts of the state of Illinois.

The holotype (female), allotype (male), and a paratype (female) are deposited in the U. S. National Museum (Cat. Nos. 81078, 81079, and 81080). Paratypes (male and female) are in the collections of Dr. H. J. Van Cleave, Dr. Arthur G. Humes, and the writer.

*Cypria mediana* sp. nov.

(Pl. VI, figs. 82-87)

*Type Locality:* Illinois.

*Description of the Female:* A species of the genus *Cypria*. Shell (fig. 82) elongate; height equal to little more than one-half the length, greatest near the center or somewhat anterior to the center. The left valve is slightly larger than the right. The dorsal margin forms a low arch, blending without interruption into the anterior and posterior margins except for a very weak sinuation which, especially in the right valve, may occur near the anterior end. The anterior and posterior ends are evenly rounded; the posterior is more narrow than the anterior. The ventral margin is concave, the concavity being deepest in the center of the posterior two-thirds of the shell. Pore-canals are present only along the ventral margin of the left valve. A hyaline border is found along the ventral, posterior, and anterior margins of each of the valves. The muscle scars are nearly centrally placed; six scars, five of which are large and one of which is inconspicuous, are found arranged in a loose group; a small isolated scar is located dorsal-anteriorly of the group while a pair of long scars are found anterior and slightly ventral of the group. A few hairs are evident along the anterior margin of the shell. Flakes of pigment may occur on the anterior and posterior slopes of the valves. The valves of three mature females from Illinois (mounted in diaphane) measure as follows:

RIGHT		LEFT	
<i>Length</i>	<i>Height</i>	<i>Length</i>	<i>Height</i>
0.94 mm.	0.50 mm.	0.— mm.	0.52 mm. (holotype)
0.90	0.54	0.91	0.58
0.88	0.48	0.90	0.49

Shell from below (fig. 83): compressed, pointed posteriorly and anteriorly; greatest width in the anterior one-half of the shell and approximately equal to two-fifths of the length.

Each antenna consists of five podomeres; the sensory organ has a length slightly less than the distal width of the third podomere. The swimming setae of the antennae extend beyond the tips of the terminal claws for a distance little longer than the length of the claws. The terminal claws and the claws of the penultimate podomere are very long and slender; the claws of the penultimate podomere reach distally beyond those of the ultimate podomere. The ultimate podomere of the mandibular palp is nearly twice as long as the width at the base; the distal claws are of greatly varying lengths, the longest at least twice the length of the ultimate podomere. The processes of each maxilla are short; the palp is of two podomeres and has the short terminal podomere distally widened, with three nearly equal spine-like setae and several smaller ones.

The second thoracic leg with the antepenultimate and penultimate podomeres equal; the ultimate podomere small, about as long as the basal width. The distal claw of the second leg is approximately equal to one and one-half times the combined lengths of the distal three podomeres. Of the two terminal setae approximate to the distal claw, one is approximately as long as the penultimate podomere, the other two-thirds as long. The third thoracic leg (fig. 84) has the antepenultimate and penultimate podomeres nearly equal in length. The ultimate podomere is but little longer than wide. Of the two unreflexed distal setae, the shorter is one and one-half to two times the length of the ultimate podomere, and the longer is twice the shorter. The distal seta of the penultimate podomere is reduced to a short spine and is surrounded by a crown of fine bristles; the lateral seta of the penultimate podomere is attached near the anterior end of the basal half of the podomere and reaches beyond the distal end of the podomere. The distal seta of the antepenultimate podomere measures between one-half and two-thirds the length of the podomere and reaches at least to the base of the lateral seta of the penultimate podomere. Lateral hairs are present along the sides of the antepenultimate and penultimate podomeres.

The ventral margin of the furca (fig. 85) is slightly curved and measures less than seven times the least width. Dorsal seta but little longer than the least width of the ramus and removed from the subterminal claw by a distance equal to a little more than twice the least width of the ramus, or about one-third of the length of the ventral margin of the ramus. The terminal claw is almost as long as the ventral margin of the ramus; the subterminal claw is four-fifths as long as the terminal. The terminal seta is equal in length to one-third of the terminal claw. Both claws are so finely toothed that superficially they appear smooth.

*Description of the Male:* Shell in general appearance like the female but smaller. The right valve (fig. 86) of the allotype (mounted in dia-

phane) measures 0.82 mm. in length and 0.44 mm. in height; the left valve measures slightly more. The testes are much larger than in most species of the genus *Cypria*. In the right valve, there is a slight sinuation at both ends of the dorsal margin. The appendages are similar to those of the female except the claw of the second leg is relatively longer. The prehensile claws and ductus ejaculatorius are *Cypria*-like and offer no special details. The penis (fig. 87) has a rather wide, flap-like, and blunt inner lobe and a narrow, chitinized middle lobe with a curved tip.

*Remarks:* *C. mediana* *sp. nov.* with the exception of two or three details of structure fits into the genus *Cypria* as usually diagnosed. The shell is more elongate than is usual in individuals of the genus and the two distal setae belonging to the pair on the ultimate podomere of the third leg are more unequal in length, resembling a *Candona* species in this respect. However, the nature of the setae of the penultimate podomere of the third leg is typically that of a *Cypria* species. The male sexual organs are those of the subfamily Cyclocyprinae. The placing of this species in the genus *Cypria* has made necessary certain relatively unimportant emendations to the genus. These have been discussed under the diagnosis of the genus.

*Ecology:* Of the three collections made by the writer containing *C. mediana* *sp. nov.*, one came from a grass covered area in an ox-bow, one from water plants in a pool of a dried up stream, and the third from water plants and old leaves along the edge of a sluggish vernal stream. Individuals of this species seem to tolerate an acid environment. All of the individuals taken were mature and were taken in the first ten days of June, 1940.

*Distribution:* This species is known only from southern Illinois, having been taken by the writer in a single collection from Johnson County, one from Marion County, and a third from Massac County, Illinois. The writer has not found this species in the northern one-half of the state.

The holotype (female) and allotype (male) of this species are deposited in the U.S. National Museum (Cat. Nos. 81081 and 81082). One paratype (female) is in the collection of Dr. H. J. Van Cleave and paratypes of both sexes are retained in the writer's collection.

### *Cypria obesa* Sharpe 1897

(Pl. VII, figs. 88-89)

*Cypria obesa* Sharpe 1897. Sharpe, 1897:462-463, pl. 48, figs. 1-5; 1918:821, figs. 1285a, b, c, d; Furtos, 1933:466-467, pl. 15, figs. 1-7.

*Type Locality:* Havana, Mason County, Illinois.

*Description of the Female:* A *Cypria* species. Shell (fig. 88) brownish in color, plump; suboval with nearly straight ventral margin. Height

about three-fifths of the length. Length varies from 0.74 to 0.86 mm., height from 0.44 mm. to 0.52 mm. The sensory organ on the inner edge of the third podomere of the antenna short; natatory setae extend beyond the tips of the terminal claws by twice the length of the claws. Last podomere of the third thoracic leg (fig. 89) slightly longer than wide; shortest distal seta equal to the length of the ultimate podomere; the longer of the pair twice the shorter. The distal seta of the penultimate podomere of the third leg much reduced and surrounded by a crown of fine bristles. Furca with terminal claw three-fifths as long as the ramus. Terminal seta about one and one-half times the least width of the ramus and the dorsal seta about as long as the width of the ramus. The dorsal seta is located a distance of three times the least width of the ramus from the subterminal claw.

*Description of the Male:* Slightly smaller than the female, otherwise similar. Prehensile palps dissimilar and unequal. Penis triangular with two subequal terminal lobes.

*Remarks:* The writer's specimens are identical with those described by Sharpe with the exception that the furcal ramus has a smooth dorsal margin instead of the toothed margin as described by Sharpe (1897). Furtos (1933) also noticed this incompatibility between her specimens and the description of Sharpe.

*Ecology:* Sharpe (1897) took this species from the sandy shore of a lake in central Illinois and Furtos (1933) reports it from a stone-quarry pool and a cold spring in Ohio. The present writer has found it as a rule associated with submerged grasses and water plants in shallow water, more often than not over a mud bottom. In fact, in seven out of eight places where this species was collected, there was an abundance of vegetation, as is common along the edges of river backwaters, swamps, and temporary vernal pools. In one instance, this species was taken from a muddy pool where there was no vegetation but as this pool was a remnant of a much larger one, it is entirely possible that this form was merely a survivant. All of the collections containing this species were made in quiet waters except that one collection was made from weeds and old leaves in a small stream not over five feet wide and having a very slow current and another was from the edge of Rock River where there was little current. This species seems to be characteristic of the aestival season rather than the vernal as is common with many Cypria species.

*Distribution:* This species has been previously reported from Havana, Mason County, Illinois, by Sharpe (1897); from Jackson Park, Chicago, Illinois, by Sharpe (1910); and from Newark and Granville, Ohio, by Furtos (1933). The present writer has collected *C. obesa* from six counties in Illinois. With the exception of Massac County which is at

the southern tip of the state, all of the Illinois reports for this species are from the northern one-half of the state.

*Cypria maculata* sp. nov.

(Pl. VII, figs. 90-95)

*Cypria opthalmica* (at least in part) Turner 1895 (*non* *C. opthalmica* (Jurine 1820)). Turner, 1895:306, pl. 75, figs. 1-3, 7; pl. 76, figs. 1-3, 5.

*Cypria opthalmica* Sharpe 1897 (*non* Jurine 1820). Sharpe, 1897:466-468, pl. 47, fig. 5; Kofoed, 1908:258.

*Cypria opthalmica* (at least in part) Sharpe 1918 (*non* Jurine 1820). Sharpe, 1918:821, figs. 1284a, b, c, d.

*Type Locality:* Illinois.

*Description of the Female:* A species belonging to the genus *Cypria*. Shell (fig. 90) from the side reniform; the dorsal margin forming a high arch slightly flattened anteriorly where it passes into the anterior margin near the eye. The anterior and posterior margins rounded, the posterior more broadly so. The ventral margin is nearly straight. The pore-canals are very short as a result of the proximity of the submargin and margin; the hyaline border of the valves common to many species of *Cypria* is absent. The muscle scars are nearly centrally located. From above, the shell appears compressed, greatest width less than the greatest height but more than one-half of the length of the shell; "widest at the posterior third, narrow, somewhat acutely pointed anteriorly and rounded posteriorly" (Sharpe, 1897). There are a few hairs scattered over the surface of the valves and each valve is marked with three irregular brown to reddish-brown blotches. One of these is on the anterior slope of each valve, another along the dorsal margin behind the eye, and the third is on the posterior slope of each valve. The length and height of several valves of mature females are as follows:

RIGHT		LEFT	
<i>Length</i>	<i>Height</i>	<i>Length</i>	<i>Height</i>
0.54 mm.	0.37 mm.	0.54 mm.	0.38 mm. (holotype)
0.54	0.38	0.54	0.39
0.55	0.38	0.56	0.39
0.50	0.34	0.50	0.35
0.48	0.33	0.48	0.34

The swimming setae of the antennae extend beyond the tips of the distal claws for a distance equal to three times the length of the distal claws. The sensory organ of the antenna has a length less than one-half of the length of the podomere which bears it. The terminal podomere of the mandibular palp is very long, being three times as long as the greatest width; distally it is only about one-half as wide as proximally.

The ultimate podomere bears, among others, two long setae which are at least one and one-half times as long as the ultimate podomere. On the outer margin of the penultimate podomere of the mandibular palp near the distal end is a group of four long setae which reach considerably beyond the distal margin of the ultimate podomere. The second thoracic leg with the proximal width of the ultimate podomere equal to or greater than the length of the podomere; terminal claw slightly less or equal in length to the sum of the lengths of the distal three podomeres. Antepenultimate podomere with a length equal to that of the penultimate podomere.

The penultimate podomere of the third thoracic leg (fig. 91) has a length little more than three times the greatest width and is longer than the antepenultimate podomere; the seta of the penultimate podomere arises proximal to the center of the podomere and reaches nearly to the level of the distal end of the podomere. The seta of the antepenultimate podomere reaches over a third of its length beyond the base of the seta of the penultimate podomere. A crown of bristles is present at the distal outer margin of the penultimate podomere but does not surround a distal seta as happens in many Cypria species. One of the seta of the crown is enlarged and spine-like. The ultimate podomere is a little longer than wide; the ventral margin is sinuated. Sharpe (1897) writes that the inner margin of the ultimate podomere of the third leg is sinuated; evidently he made an error in orientation of the appendage. The terminal setae of the similarly directed pair are nearly equal and but little longer than the length of the ultimate podomere which bears them. The furca (fig. 92) is somewhat curved; the length of the ventral margin is between seven and eight times the least width of the ramus. The margin of the ramus is smooth. The dorsal seta has a length less than the least width of the ramus and is removed from the subterminal claw by a distance equal to three times the least width of the ramus, being, therefore, nearer the midpoint of the dorsal margin than the distal one-third. The terminal seta is longer than the dorsal seta, having a length nearly twice the least width of the ramus. The terminal claw is gently curved and smooth. It has a length equal to five-eighths of the ventral margin of the ramus or about one-half of the dorsal margin. The subterminal claw measures a little more than three-fifths of the terminal claw and is very heavily toothed.

*Description of the Male:* Shell of the male the same size and shape as that of the female. The appendages are similar. Ductus ejaculatorius (fig. 93) elongate and with the general characteristics of the subfamily. Prehensile palps dissimilar and unequal. The right palp (fig. 94b) is stout, distally enlarged, with the propodus terminating in a distal process

extending beyond the dorsal margin of the heavy, hook-like dactylus. The left palp (fig. 94a) is more slender than the right, the propodus is not distally enlarged and the dactylus is narrow and distally reflexed. The penis is wide (fig. 95), with the middle lobe tapering, flap-like; the inner lobe much more slender, somewhat curved distally, having the outer margin chitinized, and shorter than the lappet-like middle lobe.

*Remarks:* It is unfortunate that Turner (1895) and Sharpe (1897) confused this species with the true *C. ophthalmica* described by Jurine in 1820. While certain similarities do exist, there are many conspicuous differences. G. W. Müller (1912) questioned the identification of *C. ophthalmica* as made by Turner in 1895. At the same time, Müller omitted entirely Sharpe's reference of 1897 to *C. ophthalmica* from Illinois. Whether this omission was intentional because he doubted Sharpe's identification or whether it was an oversight on Müller's part cannot now be ascertained. Though *C. ophthalmica* and *C. maculata* are closely related species, they may be separated definitely upon the following characters:

	<i>C. ophthalmica</i> (Jurine 1820)	<i>C. maculata</i> sp. nov.
Shell length, female.....	Seldom under 0.55 mm.	Seldom over 0.55 mm.
Color of shell.....	Most of shell covered with isolated colored patches	Three definite colored patches or areas
Antenna, sensory organ.....	$\frac{3}{4}$ length of its podomere; almost reaches distal end of podomere	$\frac{1}{2}$ length of podomere and does not almost reach distal end of podomere
Third leg, distal seta of penultimate podomere.....	Reduced to a spine surrounded by a crown of bristles	Small, a part of the crown of bristles
Furca, length of dorsal seta.....	Almost twice the least width of the ramus	About the same as the least width of the ramus
Furca, dorsal margin.....	Toothed	Smooth
Furca, subterminal claw.....	Weakly toothed	Heavily toothed
Right prehensile claw of male.....	Propodus not much enlarged distally	Propodus much enlarged distally

There is a remote possibility that *Cypria maculata* sp. nov. should be referred to *Physocypria dentifera* (Sharpe 1897) G. W. Müller 1912. The absence, however, of the definite "tuberculiiform teeth" (Sharpe, 1897) on the anterior margin of the left valve, the absence of the hyaline border along the anterior of the right shell margin, and the greater size of the shell would certainly be sufficient reason for recognizing *Physocypria dentifera* and *Cypria maculata* as apparently separate species. Occasionally a right valve of *C. maculata* may be found bearing on the anterior margin rudimentary tubercles but the writer has never found such tubercles on the margin of the left valve. As the writer has no individuals

of *Physocypria dentifera* for comparison with *Cypria maculata*, it is impossible to determine the exact relationship between the two species. Whether or not *Physocypria dentifera* represents a variable series which includes *Cypria maculata* will depend upon a detailed study made from an abundance of material of both species. Until such a study is made, Sharpe's *Physocypria dentifera* and the writer's *Cypria maculata* must stand as valid species.

*Ecology:* Unlike the closely related species *C. ophthalmica*, *C. maculata* sp. nov. is usually found in clean, alkaline waters. It may be found in vernal ponds, the shores of lakes, and along the edges of streams where the current is slowed up by the presence of aquatic plants. It seems to prefer habitats where there are algal masses, grasses, and water plants and is only in rare instances found associated with decaying vegetation.

*Distribution:* Through the uncertainty of the exact designation of *C. ophthalmica* as used by Sharpe (1918), it is impossible to give the corrected distribution for this species. Sharpe (1918) gives the distribution as Georgia, Illinois, Minnesota, and Oregon for *C. ophthalmica*, but since Sharpe's conception of *C. ophthalmica* was probably a mixture of the true *C. ophthalmica* of Jurine and what is herein designated as *C. maculata* sp. nov., the distribution records are almost valueless. The present writer has taken this species from counties in nearly all parts of Illinois.

The holotype (female) and allotype (male) of this species are deposited in the U. S. National Museum (Cat. Nos. 81083 and 81084). Paratypes (male and female) are in the collections of Dr. H. J. Van Cleave, Dr. Arthur G. Humes, and the writer.

*Cypria ophthalmica* (Jurine 1820) Brady and Norman 1889

(Pl. VII, figs. 96-97)

*Monoculus ophthalmicus* Jurine 1820. Jurine, 1820:178, pl. 19, figs. 16, 17.

*Cypria ophthalmica* (Jurine 1820) Brady and Norman 1889. Brady and Norman, 1889:69, pl. 11, figs. 5-9.

non *Cypria ophthalmica* (sic!) (in part?) Turner 1895. Turner, 1895:306, pl. 75, figs. 1-3, 7; pl. 76, figs. 1-3, 5.

non *Cypria ophthalmica* Sharpe 1897. Sharpe, 1897:466-468, pl. 47, fig. 5.

non *Cypria ophthalmica* (sic!) Sharpe 1918. Sharpe, 1918:821, fig. 1284.

*Cypria ophthalmica* (Jurine 1820) Brady and Norman 1889. Kaufmann, 1900a:336-341, pl. 20, figs. 1-3; pl. 23, figs. 15, 16; pl. 29, fig. 20.

*Cypria ophthalmica* (sic!) (Jurine 1820) Brady and Norman 1889. Sars, 1928:97-98, pl. 45, fig. 1.

*Type Locality:* Central Europe.

*Description of the Female:* An ostracod of the genus *Cypria*. Shell (fig. 96) short and high; seen from the side, the dorsal margin is strongly

arched, both anterior and posterior ends broadly rounded, the posterior more so than the anterior. The ventral margin is either straight or weakly sinuated in the center. There is a hyaline border along the anterior and posterior margins of the shell. The left valve is very slightly larger than the right. Measurements of several mature females from Illinois are as follows:

<i>Length</i>	<i>Height</i>
0.61 mm.	0.41 mm.
0.60	0.42
0.63	0.44
0.56	0.36
0.60	0.40

Surface of the valves without sculpturing but covered with pigment spots (fig. 97), each spot being made up of little flecks of pigment; these spots are usually more conspicuous along the anterior, posterior, and dorsal margins of the shell than they are in the central part of each valve.

The swimming setae of the antennae extend beyond the tips of the terminal claws a distance equal to more than three times the length of the terminal claws. The distal end of the sensory organ on the side of the antepenultimate podomere is almost at a level with the distal end of the podomere. The distal podomere of the mandibular palp is very much elongated, being three times as long as the greatest width of the podomere. The masticatory processes of the maxilla are short. The palp of the maxilla has a wide, proximal podomere and a distal podomere which is small and is attached to the ventral distal angle of the first podomere. On the distal margin, the ultimate podomere bears some bristle-like setae fully twice as long as the length of the podomere. The claw of the second thoracic leg is equal or slightly subequal to the sum of the lengths of the last three podomeres. The last podomere of the third thoracic leg is nearly as wide as long; the two shorter setae are slightly unequal, one being a little less, the other a little more than the length of the podomere to which they are attached. The penultimate podomere bears a distal seta reduced to a spine and a long seta near the basal one-third of the podomere. This latter seta reaches to the distal margin of the podomere. The margins of the penultimate and antepenultimate podomeres bear many fine hairs. The furcal ramus is stout and slightly curved. The ventral margin of the furca is approximately seven times the least width. The dorsal margin of the furcal ramus is finely toothed throughout most of its length. The apical claws are well developed, the terminal one being two-thirds the length of the ventral margin of the

ramus. The terminal seta is approximate in length to the least width of the ramus; the dorsal seta approaches twice the width of the ramus.

*Description of the Male:* The male is slightly smaller than the female. The coloration and general appearance is the same. In the male, the swimming setae of the antennae are shorter, extending beyond the tips of the terminal claws for a distance little more than twice the length of the claws. The prehensile palps are much unequal and dissimilar; the right one being much more highly developed as a prehensile structure than the left. The terminal lobes of the penis are well produced, the inner one being somewhat shorter and more acute at the distal end than the middle one. The males are not very numerous in any collection. This also has been noticed by Klie (1938a): "Die ♀♀ sind stets Zahlreicher als die ♂♂."

*Remarks:* It is very unfortunate that Sharpe (1897) mistook individuals of another species (*C. maculata mihi*) for this easily identified European species. A comparison of the species Sharpe called *C. ophthalmica* with the true *C. ophthalmica* of Jurine is made under the remarks in the description of *C. maculata* sp. nov.

Individuals assigned herein to *C. ophthalmica* agree in all important details with European descriptions of this species. The only noticeable differences are a slightly greater inequality in the two shorter distal setae of the third thoracic leg and a somewhat greater length of the dorsal and terminal setae of the furca in the American form. These differences are so slight, however, that they may be assigned to species variation. That great variation in size, shape, as well as general proportions of various structures occur in this species is well known as Kaufmann (1900a) writes: "Die Dimensionen scheinen auch bei dieser Form in den einzelnen Ländern erheblich zu differieren."

It is very improbable that *Cypria neglecta* Herrick 1879 is a synonym of *C. ophthalmica* Jurine, although both Turner (1895) and G. W. Müller (1912) consider it possible but questionable. From the size of the shell as given by Herrick (1879), "little exceeding 0.01 in.," one might reasonably suppose that Herrick examined immature individuals. His drawings (Herrick, 1879:pl. 17, figs. 2c, 2d) of the furca and the antennae ("inferior antennae") point to either immature individuals or abnormal ones although his drawing of the ductus ejaculatorius seems to be from a mature male. From the description given by Herrick, "color dull white, without markings of any kind," it is necessary to conclude that he did not have either the *C. ophthalmica* of Jurine or of Sharpe (*C. maculata*) as the color markings are without exception prominent in these two species. From Herrick's inadequate description and apparently erroneous figures,

it is not safe to reassign his *Cypria neglecta* to any known species of *Cypria*.

*Ecology:* There is a wealth of ecological data regarding this species in European waters (Kaufmann, 1900a; Alm, 1916; Klie, 1938a). In general, the species has been reported as living in "Kleineren, austrocknenden Gewässern aller Art, als auch in Grösseren Teichen und besonders am Grunde der Seen gefunden" (Alm, 1916). The present writer has collected *C. ophthalmica* only from waters which contain an abundance of decaying material and where, in some instances, the pH indicates a highly acid condition. In one collection made by the present writer from a ditch in Franklin County, Illinois, the water had a pH of 6.4. In another instance, individuals belonging to this species were collected by Robert Yapp from a cypress swamp at Reelfoot Lake, Tennessee, where the pH was 6.8. No individuals of this species have been taken from the distinctly alkaline waters of the northern part of the state of Illinois. It is evident that this species tolerates an acid condition of the water and perhaps prefers it to an alkaline condition. That this species tolerates distinctly "spoiled" waters was also noticed by Kaufmann (1900a) who writes: "Sie . . . ist sehr widerstandsfähig gegen das Verderben des Wassers, sowie gegen Temperaturunterschiede." There appears to be no seasonal restriction upon the distribution of this species.

*Distribution:* In general, this species is distributed over most of the Holarctic region and South America as well (Daday, 1905). Because of the uncertainty of Turner's identification (Turner, 1895), it is impossible to state definitely the distribution previously reported for North America. However, Turner's report of its occurrence in Georgia is probably correct. The report by Dobbin (1941) of this species in the Pacific region constitutes without doubt a valid record since her description checks closely with the present writer's. This species has been collected in several counties of central and southern Illinois. The writer has also found *C. ophthalmica* in collections made by Mr. Robert Yapp in the vicinity of Reelfoot Lake, Tennessee.

#### GENUS PHYSOCYPRIA VÁVRA 1897

The margin of either the right or the left valve has a row of tubercles or pustules which may be confined to the anterior margin alone or may be found on portions of the anterior, posterior, and ventral margins. Otherwise as in the genus *Cypria*.

Two species of this genus, *P. pustulosa* (Sharpe 1897) G. W. Müller 1912 and *P. dentifera* (Sharpe 1897) G. W. Müller 1912, are known from Illinois.

KEY TO SPECIES OF THE GENUS *PHYSOCYPRIA* IN ILLINOIS

- a. Many tubercles along the anterior margin and a few to many along the posterior margin of the right valve (fig. 98); terminal claw of the furca equal approximately to one-half of the length of the ramus.....*P. pustulosa* (Sharpe 1897) G. W. Müller 1912
- b. Many fine tubercles along the anterior margin only of the left valve; terminal claw of the furca approximately equal to three-fifths of the length of the furca.....*P. dentifera* (Sharpe 1897) G. W. Müller 1912

*Physocypria pustulosa* (Sharpe 1897) G. W. Müller 1912

(Pl. VII, fig. 98)

*Cypria pustulosa* Sharpe 1897. Sharpe, 1897:461-462, pl. 48, figs. 6-10; Kofoid, 1908:258.*Cypria (Physocypria) pustulosa* Sharpe 1897. Sharpe, 1918:821, figs. 1284a, b, c, d, e.*Physocypria pustulosa* (Sharpe 1897) G. W. Müller 1912. G. W. Müller, 1912:134; Furtos, 1933:470, pl. 16, figs. 10-11.*Physocypria globula* Furtos 1933. Furtos, 1933:468-469, pl. 16, figs. 1-9.*Type Locality:* Mason County, Illinois.

*Description of the Female:* An ostracod of the genus *Physocypria*. The subovoid shell (fig. 98) shows considerable variation in both size and shape. The dorsal margin forms a high arch. Both the anterior and posterior margins are rounded, the posterior more broadly. The ventral margin is usually nearly straight but may have a slight centrally located sinuation. The left valve is slightly larger than the right. The greatest height of the shell is about two-thirds of the length and is at the center of the dorsal margin or slightly anterior or posterior to the center. Seen from above the shell is compressed with the greatest width considerably less than the greatest height. Several shells of mature females from Illinois measure as follows:

<i>Length</i>	<i>Height</i>
0.52 mm.	0.40 mm.
0.56	0.42
0.59	0.43
0.49	0.31
0.48	0.36
0.62	0.46
0.48	0.30

The shell is moderately hairy; the eyespot is very large; the shell is marked with brown or reddish-brown blotches or patches. One of these is located anteriorly, another above and posterior to the eyespot, and the third is on the posterior part of the shell.

The most important single criterion of this species is the presence of tubercles upon the margin of the right valve. These tubercles are

highly variable in position, number, and size. The tubercles on the anterior margin of the shell are rather small and range from as few as ten to as many as twenty-five in number. A few of them may pass around the margin of the valve to the anterior end of the ventral margin. The tubercles are usually largest in the center of the row and become weaker toward the two ends, the weakest of the tubercles being barely distinguishable. The tubercles of the posterior and posterior-ventral margin present still greater variability. Occasionally they are almost unrecognizable, only rudiments appearing to mark the position of the larger tubercles. In the form described by Sharpe as *C. pustulosa* (Sharpe, 1897) there are three or four tubercles just posterior to the ventral sinuation. These are commonly not conical but are flattened and pointed posteriorly. On the right valve of other individuals (designated as *C. globula* by Furtos (1933)) these few large tubercles are followed posteriorly by a row of small, distinct tubercles along the posterior margin. The number and size of these tubercles vary; there may be only one or two or there may be nearly as many as there are tubercles on the anterior margin of the valve. With respect to the tubercles there appears to be no dividing line between the *pustulosa* form of Sharpe and the *globula* form of Furtos. This is considered further under the heading "remarks."

The swimming setae of the antennae are long, reaching a distance equal at least to three times the length of the terminal claws beyond the tips of the claws. The sensory organ of the third podomere is rather short, reaching only to the distal one-fourth of the podomere. The terminal podomere of the maxillary palp is nearly square in outline and bears distally three well developed but unequal setae and several smaller ones. The terminal podomere of the third thoracic leg is but little longer than wide. The two short distal setae are subequal, the longer one being slightly longer than the ultimate podomere of the leg. The penultimate podomere of the third leg has a long seta with the base just below the middle of the podomere and the tip reaching to the distal margin of the podomere. The podomere bears at the distal end a very small, vestigial seta and a crown of fine bristles. The inner margin of the antepenultimate and ultimate podomeres of the third leg bear numerous long hairs. The furca is long and narrow, the ventral margin usually eight to nine times as long as the least width of the slightly curved ramus. The dorsal seta varies from about one to one and one-half times the least width of the ramus and is located a little distal of the center of the dorsal margin of the ramus. The terminal seta is usually a little longer than the dorsal one. The terminal claw has a length equal to approximately one-half the length of the dorsal margin of the ramus. The sub-

terminal claw is about two-thirds the length of the terminal one. The terminal and subterminal claws are gently curved; the terminal is smooth, the subterminal has a row of fine teeth near the tip.

*Description of the Male:* The male is somewhat smaller than the female; otherwise similar. The prehensile palps are Cypria-like and are of little distinctive taxonomic importance. The penis has the outer lobe wanting; the inner lobe is relatively long, pointed, and curved; and the middle lobe is rather flap-like, not very wide, blunt at the distal end, and reaches about the same level distally as the inner lobe.

*Remarks:* *Physocypria pustulosa* is an extremely variable species of ostracod. The variation is evident in the shell shape; length to height ratio of the shell; the number, position, and size of the tubercles on the shell; the lengths of the setae on the third thoracic leg; and the lengths of the dorsal and terminal setae of the furca. In working with several hundred individuals selected from one hundred and thirty collections, the writer has found it impossible to divide the variable series representing this species into either morphological species or subspecies. It is possible, as Furtos (1933) may have done, to select individuals from the ends of the series and set them aside as different species based entirely upon the number and arrangement of the tubercles of the shell margin. However, when a large series is at hand, it is evident that *P. globula* Furtos 1933 and *P. pustulosa* (Sharpe 1897) are really a single species. In most population samples, it is possible to find individuals which have the typical *pustulosa* type of posterior-ventral tubercles and have in addition a few extremely small, rudimentary tubercles which might easily be overlooked. Very often, the number of pustules or tubercles on the anterior margin of the shell is distinctly too many for Sharpe's species and corresponds accurately with the number given by Furtos for the *globula* type. Posteriorly, however, the same shell may have only three large flattened pustules which are distinctly of the *pustulosa* type. In contrast, there may be several tubercles posteriorly as in Furtos's species with only a very few anterior ones as in Sharpe's species. The size of the tubercles also varies from heavy to practically indistinguishable. In many of the collections it is possible to find individuals which would be readily identified as *P. pustulosa* and some of which must be assigned to *P. globula*. In collections where two or more slides are available, it was found that upon initial examination of the material, the writer was confused and often placed one slide in the *pustulosa* group and the other slide in the *globula* group. This sorting was done upon the basis of the nature of the tubercles.

It was thought by the writer that there might be some structure other than the tubercles which would offer a definite and decisive criterion for

the separation of the species of Sharpe and that of Furtos. The writer was unable to find any such criterion and was indeed unable to find any correlation between the tubercles and the other variable characteristics of the species. In comparing the description of *P. globula* and *P. pustulosa* as given by Furtos (1933) the writer found the following differences, each of which, upon proper examination, is found to have no specific value in differentiating between the two described species:

(1) *P. globula* is said to measure 0.63 mm. in length and 0.41 mm. in height; *P. pustulosa* measures 0.62 mm. in length and 0.45 mm. in height. The writer has found that intermediates occur between these two sizes and the differences in height as well as the length to height ratio is not as large as the differences which occur in many of the more definitely limited species of Cypria. The difference in height and length to height ratio may then be dismissed as having no specific significance.

(2) For *P. globula*, Furtos gives 20 to 25 tubercles on the anterior end and three large tubercles followed posteriorly by many small ones at the posterior end; in *P. pustulosa* 12 to 17 tubercles at the anterior end and two or three large pustules at the posterior end of the ventral margin. As explained above, intergradations between the two described forms occur.

(3) According to Furtos, the longer of the pair of terminal setae of the third leg of *P. globula* is one and one-half times the length of the ultimate podomere; the longer in *P. pustulosa* is but slightly longer than the podomere. This difference is not at all significant as variation beyond these limits is not uncommon in many ostracod species. Moreover, there seems to be no correlation between the number of tubercles and the relative length of the distal setae of the third thoracic leg.

(4) The furcae, according to Furtos's descriptions, differ in some few details in the two forms. In *P. globula* the furca is said to have a length eleven times the least width of the ramus, while in *P. pustulosa* the length is nine and one-half times the least width. If one assumes that camera lucida drawings are more accurate than text descriptions, then it is apparent by measuring the drawing (Furtos, 1933:pl. 16, fig. 6) that the text description of the furca of *P. globula* is incorrect and the correct length-width ratio is more nearly nine and one-half than eleven. One may say then that there is no significant difference between the length-width ratios of the furcal rami of the two forms under discussion.

(5) Another apparent difference between the descriptions of the two species given by Furtos is that the dorsal seta of the furca in *P. globula* is removed from the distal end of the ramus by one-third of the dorsal margin of the ramus, while the dorsal seta of *P. pustulosa* is removed from the distal end of the ramus by about two-fifths of the dorsal margin of the ramus. Referring to Furtos's drawing (her pl. 16, fig. 6) of the

furca of *P. globula*, it is apparent that the dorsal seta is removed from the distal end of the ramus by at least two-fifths of the dorsal margin of the ramus. This, then, is not a significant difference between the two species.

(6) While Furtos states that the male structures are similar in *P. globula* and *P. pustulosa*, she gives the size of the former as being 0.62 mm. long and 0.39 mm. high while the latter is 0.55 mm. long and 0.39 mm. high. Such size variation has no specific significance especially since it is not correlated with any other characteristic.

The above discussion conclusively shows that the species *P. globula* can be nothing else than the end of the series which represents *P. pustulosa*. *P. globula* Furtos 1933 then becomes a synonym of *P. pustulosa* (Sharpe 1897).

Whether or not there may be local races of individuals clustered about one end of the series representing *P. pustulosa* is possible but not definitely known. The discovery and study of such races will not, the writer believes, destroy our conception of *P. pustulosa* as it now stands, but may add something to the knowledge of variation and species development in the Ostracoda.

*Ecology:* In general, *Physocypria pustulosa* prefers the quiet waters of lakes especially in areas where there is an abundance of plant life. It is occasionally found in roadside ditches over apparently bare bottom and is sometimes a constituent of plankton. The abundance of individuals of this species seems to reach a peak in June with the individuals becoming less abundant in July and August.

*Distribution:* *P. pustulosa* has been reported under the names *P. globula* and *P. pustulosa* by Furtos (1933) from various places in Ohio. Dobbin records it as *Cypria* (*Physocypria*) *globula* from Washington and Alaska. It was reported from Illinois by Sharpe (1897) and Kofoid (1908). It has been taken by the present writer in all parts of the state. When sufficient collections have been made, records of the distribution will probably be extended to all counties of the state.

*Physocypria dentifera* (Sharpe 1897) G. W. Müller 1912

*Cypria dentifera* Sharpe 1897. Sharpe, 1897:463-465, pl. 47, figs. 6-11; 1908:400, 410, pl. 50, figs. 3, 4.

*Cypria* (*Cypria*) *dentifera* Sharpe 1897. Sharpe, 1918:820, figs. 1282a, b, c, d.

*Physocypria dentifera* (Sharpe 1897) G. W. Müller 1912. G. W. Müller, 1912:133; Furtos, 1933:468.

*Type Locality:* Cincinnati, Ohio.

*Description of the Male and Female (after Sharpe, 1897):* Shell highest just posterior to the center; anterior and posterior ends rounded,

the posterior more broadly. The ventral margin has a slight sinuation near the center. The shell has dark brown markings distributed as follows: one anterior, one ventral, one "dorsal-ventral," and one vertical just posterior to the eye. Few hairs except at the anterior and posterior margins. "The anterior margin of the right valve projects as a hyaline flange, receiving as in a pocket the anterior margin of the left valve, which is armed with a row of eighteen to twenty tuberculiform teeth." Swimming setae of the second antennae reaching beyond the terminal claws a distance equal to the entire length of the antennae. Second thoracic legs stout; terminal claw much bent and as long as the last three podomeres together; the distal seta of the antepenultimate podomere two-thirds as long as the podomere. The two short setae of the third thoracic legs are approximately equal to each other and to the last podomere; the distal podomere has a sinuation on its inner edge and is two-thirds as wide as long; penultimate podomere three and three-fourths times the length of the terminal one, a plumose seta is found at its "middle point" and a comb of bristles is located distally. The antepenultimate podomere of the third thoracic leg as long as the penultimate; the rather stout seta at the distal inner angle is as long as the seta on the penultimate podomere. Caudal rami stout, about ten times as long as wide. Terminal claw three-fifths as long as the ramus; subterminal one two-thirds as long as the terminal one with a comb of long teeth near the tip. Terminal seta equals one-half of the subterminal claw in length; dorsal seta not longer than the least width of the ramus and located slightly above the center of the ramus.

*Remarks:* The exact identity of *Physocypria dentifera* is somewhat obscure as Sharpe seems to have been the only individual to see representatives of this species. This species, as far as appendages are concerned, bears a very close resemblance to *Cypria maculata mihi*. The principal differences between *Physocypria dentifera* and *Cypria maculata* are that the shell of the latter is smaller, the anterior margin of the left valve is not tuberculate or crenulate, and the right valve has no hyaline border. Occasionally individuals assignable to *C. maculata* may have a roughened area along the margin of the left shell but never teeth in the position, number, or shape shown by Sharpe (1897:pl. 47, fig. 6). It is possible that Sharpe worked with material which showed a development of this roughened margin into tubercles or Sharpe may have made an inaccurate observation of the true condition. Like Furtos (1933), the present writer has found no individuals assignable to *Physocypria dentifera*. As a result of a lack of material, it is impossible to compare in detail *Physocypria dentifera* and *Cypria maculata*. When such material is available, it

may be possible to show that *Physocypria dentifera* and *Cypria maculata* both belong to a series which represents a single species under the valid name of *Physocypria* or *Cypria dentifera* Sharpe 1897.

*Ecology:* Nothing is known of the ecology of *Physocypria dentifera* except that it was found in ponds by Sharpe (1908).

*Distribution:* Sharpe (1897) originally described this species from Ohio. Later he (Sharpe, 1908) gave as new records New York and New Jersey. In the same report (1908) but in the introduction, Sharpe lists Illinois, Ohio, New York, and New Jersey as the localities from which he had examined material in the U. S. National Museum. Nowhere does he give any information concerning the locality from which the Illinois material was taken. The present writer has found no individuals of this species in his collections from Illinois.

#### SUBFAMILY ILYOCYPRINAE

Shell oblong to subrectangular, dorsal margin usually straight and horizontal (figs. 99, 101); shell always possessing small pits, with one or more transverse median depressions, often with larger rounded hump-like projections and marginal spines. Antennules with some of the swimming setae shortened and claw-like. Swimming setae of the antenna always present, but may be greatly shortened. Antennae in male without special setae. The endopodite of the first thoracic leg not strongly developed in the female but consisting of two or three podomeres and clearly leg-like; in the male larger and transformed into a prehensile palp of two podomeres; respiratory plate well developed with six setae. Ultimate podomere of the third leg cylindrical with three setae, the longest of which may or may not be reflexed. Furca always well developed. Ductus ejaculatorius with numerous, crowded chitinous rods and with spherical inflated opening at each end. Penis with a clearly twisted vas deferens.

A single genus *Ilyocypris* belongs to this subfamily. Daday in 1900 introduced a second genus *Iliocyprilla* to include *I. bradyi* and related species in which the swimming setae of the antennae are reduced and the penultimate podomere of the second leg is divided. Species like *I. gibba* with long swimming setae on the antenna and the third leg with the penultimate podomere undivided were left in the genus *Ilyocypris* s. str. Few writers have followed Daday's division of the group. Among those advocating this division is Sars (1928) who believes that *Iliocyprilla* should be retained as the differences between *Iliocyprilla* and *Ilyocypris* involve characters to which "generally a generic value has been assigned" (Sars, 1928). However, the characters used for generic diagnosis vary in different individual instances. The divided or undivided condition of

a podomere of a leg may occur in different species of the genus *Candona* and yet assignment to that genus is not questioned. The relative length of the swimming setae has little significance since considerable variation of length of setae is shown within many genera. The general appearance of the shell and appendages is so similar in *Iliocypris* and *Ilyocypris* and most of the useful taxonomically important structures are so alike that there is little justification in accepting the genus *Iliocypris*.

#### GENUS ILYOCYPRIS BRADY AND NORMAN 1889

With the characters of the subfamily.

#### KEY TO SPECIES OF THE GENUS ILYOCYPRIS IN ILLINOIS

- a. Shell with three pairs of distinct lateral projections (fig. 99-P); swimming setae of antennae reach considerably beyond the end-claws; penultimate podomere of the second leg undivided (leg of four podomeres) (fig. 100) ..... *I. gibba* (Ramdohr 1808) Brady and Norman 1889
- b. Shell without well developed lateral projections, but with two shallow lateral furrows on each valve (fig. 101); swimming setae of the antennae short, almost claw-like; penultimate podomere of the second leg distinctly divided (leg with five apparent podomeres) (fig. 102-P) ..... *I. bradyi* Sars 1890

*Ilyocypris gibba* (Ramdohr 1808) Brady and Norman 1889

(Pl. VII, figs. 99, 100)

*Cypris gibba* Ramdohr 1808. Ramdohr, 1808:91, pl. 3, figs. 13, 14, 17.

*Ilyocypris gibba* (Ramdohr 1808) Brady and Norman 1889. Brady and Norman, 1889:107, pl. 22, figs. 1-5; Sharpe, 1908:410-411, pl. 56, figs. 1, 2; 1918:809, figs. 1257a, b; Furtos, 1933:427, pl. 1, figs. 4-7.

*Type Locality:* Europe.

*Description of the Female:* A species of the genus *Ilyocypris*. Shell in side view (fig. 99) with the greatest height in the region of the eye and almost equal to one-half the length. The dorsal margin nearly straight; ventral margin distinctly sinuated in the center. The anterior end appears larger and the margin more broadly rounded than the posterior. At the anterior and posterior ends of the shell there are usually conspicuous spines often set back from the margin. Three large lateral projections are found on each valve (fig. 99-P): one slightly anterior to the center of the shell and often coinciding with the muscle scars, the second dorsal and posterior to the first, and the third and smallest ventral and posterior to the center of the valve. These projections may be somewhat reduced in a small percentage of individuals. Two furrows (fig. 99-F) lie dorsal and anterior to the dorsal-anterior projection. These furrows are posterior to the eye and extend to the dorsal margin of the shell. The

surface of the shell and the margins bear numerous hairs. From above, the two most dorsal projections are easily observed on the sides of the shell. The greatest width is less than the greatest height and is posterior to the center of the shell. The length of the females vary greatly, the average being a little less than 0.95 mm.

Swimming setae of the antennae well developed but variable; usually the distal one-third of the setae extends beyond the end claws of the antennae. Penultimate podomere of the second thoracic leg (fig. 100) undivided, the leg being composed of four podomeres. Furcal ramus stout; the ventral margin a little less than twelve times the least width of the ramus; ramus gently curved with the dorsal margin spined. The dorsal seta has a length approximately equal to four times the least width of the ramus and is removed from the subterminal claw by a distance nearly equal to the length of the seta. The terminal claw is almost as long as two-thirds of the ventral margin of the ramus; the subterminal claw is little shorter than the terminal. The terminal seta has a length subequal to twice the least width of the ramus.

*Description of the Male (mainly after Klie, 1938a):* The shell of the male is said to be much like that of the female in shape and size. The furca of the male is more strongly curved than in the female. The two prehensile palps are similar; the propodus is long and cylindrical and the long dactylus tapers to an acute point. The middle lobe of the penis is much larger than the other lobes; it is lappet-like and the distal-inner corner is in the form of a right angle. Males have been found in northern Africa and in southeastern Russia. Males have not been reported from North America and none were found in the present writer's collections.

*Remarks:* The earliest reference to this widely distributed species in North America is that of Sharpe (1908) who reported *I. gibba* from Colorado. It seems rather strange that Sharpe (1897) did not find *I. gibba* in Illinois when it is now known to be very abundant. That Sharpe did not find this species in Illinois may be the result of examining little else than material collected from ponds and lakes rather than rivers and streams where it commonly occurs.

*Ecology:* *I. gibba* is a very common species found chiefly in running waters. That it is seldom found in lakes and ponds is shown by its occurrence in such habitats in only three of the forty-four collections made by the writer; the other forty-one collections were taken from streams, rivers, and pools in stream beds. *I. gibba* is found for the most part associated with vegetation and algae in current which, in some instances, is very swift. This is in contrast to the habitat reported as "sandy bottoms of large and small lakes" by Furtos (1933). It is possible that few of her collections were made from streams since this type of habitat

is usually not considered profitable for collecting ostracods. Sars (1928) reports *I. gibba* as being common in shallow ponds and "ditches with clayey bottom." Like most writers, Sars makes no mention of the occurrence in streams. G. W. Müller (1900), however, states that this species is present in every little stream as well as the backwaters of rivers and widened, shallow places in streams. It is found where the bottom mud is not too slimy and soft. The waters in which *I. gibba* is found are usually permanent but this species may at times be found in habitats, especially small vernal streams, which completely dry up in July and August. In consideration of the types of vegetation in the habitats from which this species was collected, *I. gibba* is found most abundantly in grass growing either in the water along the edge of the stream or growing on the bank and falling over into the water. In about fifteen per cent of the collections, *I. gibba* was found on the bare bottom and in about twenty-eight per cent of the collections, this species was taken from algal masses. In regard to seasonal distribution, *I. gibba* appears most abundant in the late vernal and in the aestival seasons. It was not taken by the writer earlier than May.

*Distribution:* *I. gibba* has been reported throughout the Holarctic region. In the United States, it was first reported from Colorado by Sharpe (1908). It has recently been recorded from Ohio by Furtos (1933). The species is more abundant and widespread than generally understood, having been taken by the present writer from counties in all parts of Illinois but with greater frequency in the northern than in the southern one-half of the state.

*Ilyocypris bradyi* Sars 1890

(Pl. VII, figs. 101, 102)

*Ilyocypris bradyi* Sars 1890. Sars, 1890:59-60; Sharpe, 1908:411-412, pl. 56, figs. 3-6; 1918:810, figs. 1258a, b, c, d.

*Ilyocypris bradii* (sic!) Sars 1890. Furtos, 1933:428, pl. 1, figs. 8-10.

*Type Locality:* Norway.

*Description of the Female:* A species belonging to the genus *Ilyocypris*. Subrectangular shell (fig. 101) with straight, almost horizontal, dorsal margin. Greatest height in the region of the eye and scarcely more than one-half of the length. Two distinct dorsal-lateral furrows are present between the center of the shell and the eye. The dorsal margin forms a corner with the posterior margin, giving the shell a rectangular appearance. The anterior and posterior ends are rounded, the former more broadly. The ventral margin has a conspicuous sinuation. From above, the somewhat compressed shell is narrowly oblong in shape with the anterior end pointed and the posterior end rounded, the left shell

slightly larger than the right, the sides of the valves flattened, and the greatest width hardly two-fifths of the length. A few spines, tubercles, and hairs decorate the margins. The shells of mature females usually average about 0.95 mm. in length.

The length of the swimming setae of the antennae seldom reach much beyond the middle, never beyond the distal margin, of the penultimate podomere of the antenna. The second thoracic leg (fig. 102) has five apparent podomeres through the division of the penultimate podomere. The third thoracic leg of *I. bradyi* is similar to that of *I. gibba* but the furca differs by the ramus of *I. bradyi* being much more curved, the dorsal seta relatively smooth and straight, and the terminal seta little exceeding the least width of the ramus. Otherwise similar to *I. gibba*.

*Males:* Concerning the males, Furtos (1933) says: "Male not recorded for Ohio. Rare elsewhere." The present writer has found no males in Illinois collections and knows of no instance in the literature where males have been definitely recorded.

*Remarks:* As in the related species, *I. gibba*, Sharpe (1897) probably overlooked the present species in Illinois because he did little collecting from small streams.

*Ecology:* Like the closely related species, *I. gibba*, *I. bradyi* inhabits running waters, seldom being found in ponds or lakes. Individuals are also common in pools left in stream beds after the stream has ceased to flow in late summer. The habitat of this species is similar in nearly all respects to that of *I. gibba*, and in fact *I. bradyi* and *I. gibba* are often found associated together.

*Distribution:* *I. bradyi* is known to be widely distributed in the Holarctic region. It was first reported in the United States from Colorado by Sharpe (1908). Furtos (1933) reports it from Ohio. The present writer has taken *I. bradyi* from many counties in Illinois. The majority of these counties are from the northern part of the state, none from the extreme southern part.

#### SUBFAMILY CYPRINAE *s. str.*

A subfamily of the family Cypridae. Shell usually reniform (figs. 105, 110); height variable but in most species about one-half of the length. Swimming setae of the antennae (fig. 1-V) either well developed or reduced, generally not reaching much beyond the end points of the terminal claws. The outer masticatory process of the maxilla with two or three spine-like setae; end podomere of the maxillary palp ordinarily cylindrical, often narrowed or widened distally. First thoracic leg with endopodite of one podomere in the female; modified in the male to form a prehensile palp of two podomeres. Third thoracic leg distally beak-like,

modified for grasping; ultimate podomere with only two well developed setae, the third being small and hook-like or wanting (fig. 1-T). Furca usually well developed and having two claws and two setae with a relatively slender ramus (figs. 107, 111).

The subfamily Cyprinae *sensu lato* as ordinarily used by many authors may be broken into three subfamilies: the Cyprinae *s. str.*, the Notodrominae, and the Cypridopsinae. Following Kaufmann (1900b) and Wagler (1937), the present writer has thought it convenient as well as advisable to use the subfamily Cyprinae in the restricted sense. The subfamily Cyprinae *s. str.* includes a number of genera. As the genera are not properly limited or defined, each writer has used whatever ones he thought convenient and applicable. Members of this subfamily are found in nearly all parts of the world. The Cyprinae *s. str.* is represented in Illinois by a few species belonging to two genera: Cypricercus Sars 1895 and Cyprinotus Brady 1885.

#### KEY TO GENERA OF THE SUBFAMILY CYPRINAE IN ILLINOIS

- a. Margin of both valves of shell smooth (figs. 103, 105); the furcal ramus with a length more than twenty times the least width (fig. 107)..... Genus CYPRICERCUS Sars 1895
- b. Margin of right or left valve of shell tuberculated (fig. 110); the furcal ramus with a length less than twenty times the least width (fig. 111)..... Genus CYPRINOTUS Brady 1885

#### GENUS CYPRICERCUS Sars 1895

Shell elongate, greatest height anterior to the center and in Illinois species exceeding slightly one-half of the length. The outer masticatory process with two long, toothed spine-like setae. Furca slender (fig. 107); terminal claw with a length not more than one-half of the anterior margin of the ramus but longer than three times the length of the terminal seta. An important criterion of the genus is the coils of the testis in the anterior portion of each valve (fig. 108-A). This important criterion, however, cannot always be used since the males are in some species unknown, in other species rare. The genus is found throughout the Holarctic region.

Since males are seldom seen in many species and are unknown in others, the placing of any species into this genus depends largely upon the character of the furca which has a ventral margin measuring more than twenty times the least width of the ramus. According to Sars (1928), who originally described the genus Cypricercus in 1895 to include a South African species reproducing by syngamy and characterized by a well developed furca and the peculiar coiled arrangement of the testes, the genus should be expanded to include all the Cyprinae with the extremely long furcal rami even though the males may be unknown. Some

writers (as Furtos, 1933) choose to reserve the genus *Cypricercus* for those species in which the males are well known and to place all forms in which the males are either little known or unknown into the genus *Eucypris* even though they are, because of the slender furcal rami, closely related to *Cypricercus*. Such a system based on the method of propagation is very artificial and is certainly not the method indicated by Sars, the original designator of the genus *Cypricercus*.

#### KEY TO SPECIES OF THE GENUS *CYPRICERCUS* IN ILLINOIS

- 1a. Shell tuberculate over entire surface (fig. 103); usually under 1.00 mm. in length.....*C. tuberculatus* (Sharpe 1908) *comb. nov.*
- b. Shell not tuberculate; usually over 1.00 mm. in length.....2
- 2a. Size of shell of female usually more than 1.35 mm. in length; penultimate podomere of the antenna narrow, six times as long as wide, the seta which arises from the distal, posterior corner of the antepenultimate podomere widened at the base but not forming a spherical-shaped swelling; dorsal seta of the furca reaching only to base of the subterminal claw.....  
.....*C. fuscatus* (Jurine 1820) Sars 1928
- b. Size of shell usually less than 1.35 mm. in length; penultimate podomere of antenna only four and one-half times as long as the width (fig. 1-AN), base of seta at the distal posterior corner of the antepenultimate podomere usually swollen spherical-shaped (fig. 106-B); dorsal seta of the furca reaches beyond the base of the subterminal claw (fig. 107).....  
.....*C. reticulatus* (Zaddach 1844) Sars 1928

#### *Cypricercus tuberculatus* (Sharpe 1908) *comb. nov.*

(Pl. VII, figs. 103, 104)

*Spirocypris tuberculata* Sharpe 1908. Sharpe, 1908:406-408, pl. 50, figs. 1, 2; pl. 54, fig. 4; pl. 55, figs. 1-6; 1918:814, figs. 1267a, b, c.

*Type Locality:* Jackson Park, Chicago, Illinois.

*Description of the Female:* A species of the genus *Cypricercus*. Seen from the side (fig. 103), the shell is almost elliptical; the dorsal margin is a flattened arch which, along with the almost straight ventral margin, makes both ends appear broadly and evenly rounded, the anterior more so than the posterior. The greatest height lies near the center of the shell and is approximately four-sevenths of the length. From above, the shell is oval and very tumid; the valves are nearly the same size but the right, according to Sharpe (1908), may overlap slightly the left. In some individuals, however, the present writer has found that the left valve is the larger and overlaps the right valve at least anteriorly. The surface of the shell is covered with characteristic droplet-like papillae which are strikingly conspicuous. Most of the papillae bear fine hairs. The color is usually purplish brown with a light transverse band in the region of the eye and another light band near the posterior one-third of the shell. Usually there is a much darkened area between the two light colored

bands. Sharpe (1908) gives the shell dimensions as follows: length, 0.93 mm.; height, 0.53 mm.; breadth, 0.7 mm. Most of the writer's specimens measure 0.86 to 0.90 mm. in length and 0.49 to 0.51 mm. in height.

The swimming setae of the antennae extend but little beyond the ends of the terminal claws. The outer masticatory process of the maxilla has two claw-like toothed spines, one of which may be much more heavily toothed than the other. The pectinate claw of the second thoracic leg has a length equal to one and one-third times the sum of the lengths of the last three apparent podomeres of the leg. Furca nearly straight, slender as in other members of the genus *Cypricercus*. According to Sharpe (1908) the ratio of the length to the least width of the furca in *C. tuberculatus* is 32 to 1. This statement is not supported by his figure (1908:pl. 55, fig. 3) and it cannot be verified by the present writer who has found the ratio of the length of the ventral margin of the furca to the least width to be about 22 or 23 to 1. The dorsal margin of the furca is smooth. The dorsal seta is relatively short, reaching only to the base of the subterminal claw and being removed from the tip of the ramus by a distance equal to about twice the least width of the ramus. The terminal claw is nearly straight, obscurely pectinate near the distal end, and measuring approximately one-half the length of the dorsal margin of the furca; the subterminal claw is nearly four-fifths as long as the terminal one. The terminal seta is longer than the dorsal one, measuring about one-third as long as the terminal claw or over four times the least width of the ramus.

*Description of the Male:* The shell of the male is similar in size, shape, and sculpturing to that of the female. The appendages of the male are like those of the female. The prehensile palps have a stout propodus with a falciform dactylus. The dactylus of the right palp is larger than that of the left but somewhat similar in shape. The testes have their origin in the anterior one-half of the valves, where they occur as concentric circular figures. The ductus ejaculatorius is long and slender and has about twenty wreaths of supporting spines. The penis (fig. 104) has the middle and inner lobes well developed. The inner lobe is distally rounded while the middle lobe is truncate and extends beyond the end of the inner lobe.

*Remarks:* *Cypricercus tuberculatus* when described in 1908 was assigned by Sharpe (1908) to the genus *Spirocypris* which the same writer (1903) had previously created. Since the arrangement of the testes in *Cypricercus* is similar to that found in *Spirocypris* and the nature of the testes was the chief diagnostic character of Sharpe's genus *Spirocypris*, there is no valid reason for not absorbing his genus into the previously designated genus *Cypricercus*. The advisability of assigning the species

under discussion to the genus *Cypricercus* is substantiated by the placing of a very closely related species in the genus *Cypricercus* by Sars (1926). Sars at this time seems to have been unaware of the *Spirocypris tuberculata* of Sharpe as he says (Sars, 1926) regarding his new species, *Cypricercus horridus* Sars 1926, from Canada: "It is, however, well distinguished from any of the other known species by the very pronouncedly scabrous surface of the shell." Both *C. tuberculatus* and *C. horridus* seem to fit naturally into the genus *Cypricercus* because of the character of the furca and the arrangement of the testes. *C. horridus* differs from *C. tuberculatus* in having a shell of greater length, more overlapping of the right valve by the left, a more slender penultimate podomere of the antenna, and a furca in which the dorsal seta is much longer than the terminal one and which extends well beyond the tip of the ramus.

*Ecology:* Sharpe (1918) reports this species under the name *Spirocypris tuberculata* in "Shallow, weedy, and swampy ponds; spring." The present writer has taken this species in June from grass and algae along lake shores and from a swampy area in a small lake where there were both decaying and living plants over a mud bottom. Collections made from the same locality in August by Mr. Bertrand A. Wright and by the writer did not reveal the presence of this species.

*Distribution:* This species was reported as common by Sharpe (1908) from northeastern Illinois and northern Indiana. The present writer has taken the species only from McHenry and Lake Counties, Illinois. As far as known at the present time, *C. tuberculatus* appears to be restricted in habitat to the region of lakes of glacial origin in the Chicago area.

### *Cypricercus fuscatus* (Jurine 1820) Sars 1928

- Monoculus fuscatus* Jurine 1820. Jurine, 1820:174, pl. 19, figs. 1, 2.  
*Cypris burlingtonensis* Turner 1894. Turner, 1894:17-19, pl. 7, figs. 14-23.  
*Cyprinotus burlingtonensis* (Turner 1894) Turner 1895. Turner, 1895:333-334, pl. 70, figs. 14-23; Sharpe, 1897:435-437, pl. 42, fig. 7; Furtos, 1933:446-447.  
*non Cypris fuscata* Turner 1895 (*non* Jurine 1820). Turner, 1895:320-321, pl. 71, figs. 41-46; pl. 72, figs. 7-7p; pl. 76, fig. 9.  
*Cypris (Cypris) fuscata* (in part) (Jurine 1820) Desmarest 1825. Sharpe, 1908:403-405, pl. 53, fig. 3, *non* 1, *non* 2, *non* 4.  
*Cypris (Cyprinotus) burlingtonensis* Turner 1894. Sharpe, 1918:816, figs. 1272a, b, c.  
*Cypris (Cypris) fuscata* (in part as var. *major* G. W. Müller 1900) (Jurine 1820) Desmarest 1825. Sharpe, 1918:818, fig. 1278a, *non* b, *non* c, *non* d.  
*non Eucypris fuscata* (Jurine 1820) var. *gigantica* Furtos 1933. Furtos, 1933:451-452, pl. 4, figs. 1-4.

*Type Locality:* Europe.

*Description of the Female (chiefly after Klie (1938a)):* An ostracod of the genus *Cypricercus*. Shell in side view elongated; greatest height

just posterior to the eye and more than one-half the length. The dorsal margin forms a flat arch which passes into the broadly rounded anterior margin and the narrowly rounded posterior margin without interruption. Ventral margin usually showing a very slight sinuation. From above, the shell is oval; the greatest width in the middle and more than one-half of the length of the shell; the posterior end is rounded and the anterior is weakly pointed. Length of the shell usually between 1.4 mm. and 1.5 mm.

The swimming setae of the antennae reach beyond the distal ends of the terminal claws. The penultimate podomere of the antenna has a length equal to six times the width; posterior distal seta of the antepenultimate podomere has a tapering base. The claw-like setae of the outer process of the maxilla are toothed. The ramus of the furca is very narrow, the ventral margin having a length equal to twenty-five times the least width of the ramus. The terminal claw has a length less than one-half of the ventral margin of the ramus and the dorsal seta reaches only to the base of the subterminal claw.

*Male:* Unknown.

*Remarks:* Sharpe seems not to have recognized *C. fuscatus* as such in 1897 but he (1897) described some individuals which no doubt belonged to this species under the designation *Cyprinotus burlingtonensis* (Turner 1894) Turner 1895. At the same time, Sharpe apparently applied the name *Cypris fuscata* to what herein is designated as *Cypricercus reticulatus*. The exact identity of the *Cypris burlingtonensis* of Turner (1894) appears to have been for some time in doubt, so much in fact that G. W. Müller (1912) in the volume on ostracods in "Das Tierreich" series listed it under the heading "*Genera dubia et species dubiae Cyprinarum*." At the time of the original description of *Cypria burlingtonensis* by Turner, the descriptions of the now designated *Cypricercus fuscatus* from Europe (type locality) were so confused with other related species that he may readily have been unable to establish identity with the European *fuscata*. Thus he was forced to describe his material as a new species. The mere creation of a synonym would not have created much disturbance but Turner later (1895) changed his species *burlingtonensis* from the genus *Cypris* to the genus *Cyprinotus*. This may or may not have been correct at that time as the original diagnosis of the genus *Cyprinotus* as given by Brady (1885) was very inadequate. This incomplete generic diagnosis may have led Turner to assign his *burlingtonensis* to the genus *Cyprinotus*. The genus *Cyprinotus* has since then, however, been emended and accepted by most authors to include species which like the type species, *Cyprinotus cingalensis* Brady 1885, has a

row of denticles along the margin of the right valve, or in some species along the margin of the left valve. Evidently both Turner (1895) and Sharpe (1897) accepted the genus *Cyprinotus* without reference to the denticles of the valve margin. Sharpe (1897), however, seems to have noticed something peculiar about *burlingtonensis* since he is led to state that it "greatly resembles *Cypris fuscata* Jurine in many respects." Furtos (1933) continued to carry *burlingtonensis* without question in the genus *Cyprinotus* although she saw no ostracods in Ohio assignable to this species and even states (1933) that no mention was made by Turner of marginal tubercles. At the same time she gives as a characteristic of the genus *Cyprinotus* (Furtos, 1933) that the margin of the right valve is more or less tuberculated. Certainly there are no tubercles on the margin of the valves in Turner's *Cypris burlingtonensis*. According to recent generic diagnosis, this cannot belong to the genus *Cyprinotus*. Both the nature of the shell and the form of the furca indicate a close relationship with species of the genus *Cypricercus*. Thus *burlingtonensis* must be placed in the genus *Cypricercus*. Once this is done, it is obvious that *burlingtonensis* agrees in practically every respect with *Cypricercus fuscatus*, especially when a close study is made of Turner's illustrations (Turner, 1894:pl. 7, figs. 14-23). Not only is the identity shown by the morphological structure but some substantiation of this synonymy is offered by ecological data since both *C. fuscatus* Jurine and Turner's *Cypris burlingtonensis* are vernal species found usually in temporary pools where the animals live in the decaying vegetation of the previous summer. On the basis of the above arguments, there can be no doubt that *Cyprinotus burlingtonensis* (Turner 1894) Turner 1895 must become a synonym of *Cypricercus fuscatus* (Jurine 1820) Sars 1928.

In regard to *Eucypris fuscata* var. *gigantica* described by Furtos in 1933, it is definitely not equivalent to *C. fuscata* from which it differs in many important respects. On the basis of these differences, the present writer holds the opinion that *gigantica* should be raised from subspecific to specific rank.

Sharpe (1908, 1918) did not differentiate very clearly between the now designated *Cypricercus fuscatus* (his *Cypris fuscata* var. *major* G. W. Müller 1900) and the herein designated *Cypricercus reticulatus* (his *Cypris fuscata* var. *minor* G. W. Müller 1900), although he did recognize that the two different forms occurred. His drawings are often of the *minor* variety (*C. reticulatus*) but labeled as being of the *major* variety (*C. fuscatus*). This is unfortunate and shows perhaps that he was unable to distinguish clearly between the now designated species *C. reticu-*

*latus* and *C. fuscatus*. The following table is designated to facilitate separation of these two closely related species:

	<i>C. fuscatus</i> (Jurine 1820) Sars 1928	<i>C. reticulatus</i> (Zaddach 1844) Sars 1928
Shell:		
Size, female.....	1.4-1.5 mm. long	1.0-1.3 mm. long
Dorsal margin.....	Flat, even arch	Rounded, obtuse angle at highest point
From above.....	Anterior end more acute than posterior	Both ends equal in shape
Antenna:		
Penultimate podomere.....	Length six times the width	Length four and one- half times the width
Posterior distal seta of antepenultimate podomere.....	Tapering basal portion	Spherical basal portion
Furca:		
Ratio of length to least width of ramus	25 : 1	22 : 1
Dorsal seta.....	Scarcely reaches beyond base of subterminal claw	Extends beyond the base of the subterminal claw
Terminal claw.....	Shorter than one- half of ventral margin of ramus	Nearly equals one- half of ventral margin of ramus
Terminal seta.....	Length less than one-third of sub- terminal claw	Length more than one- third of subterminal claw

*Ecology:* *Cypricercus fuscatus* is found in grassy ponds and swamps both in North America (Turner, 1894; Sharpe, 1908) and in Europe (Klie, 1938a). This species has but a single generation each year. Individuals may be found in the prevernal, vernal, and early part of the aestival season in Illinois.

*Distribution:* *C. fuscatus* is found throughout the Holarctic region. It was reported as *Cypris burlingtonensis* by Turner (1894) from Burlington, Ohio; Atlanta, Georgia; and Kent County, Delaware. Under the same designation, Sharpe (1897) reported this species from Normal, Illinois. Later Sharpe (1908) reported this species as *Cypris fuscata* var. *major* from the region of Chicago, Illinois, and the northwestern corner of Indiana. Shelford (1913) lists *Cypris fuscata* Jurine as occurring in a temporary pond south of Jackson Park, Chicago, Illinois. Sharpe, according to a personal conversation with Dr. V. E. Shelford, identified this material and the present writer believes that it may have included both *Cypricercus fuscatus* and *C. reticulatus*. The writer has not discovered individuals of this species in his collections but this may be expected as no early spring collections were made from the region immediately southeast of Chicago, Illinois, where this species appears to be more or less localized as far as the state of Illinois is concerned.

*Cypricercus reticulatus* (Zaddach 1844) Sars 1928

(Pl. I, fig. 1; pl. VII, fig. 105;

pl. VIII, figs. 106-109)

*Cypris reticulata* Zaddach 1844. Zaddach, 1844:34; Sharpe, 1897:441-442, pl. 43, figs. 3, 4.*Cypris affinis* S. Fischer 1851. S. Fischer, 1851:160, pl. 10, figs. 9-11.*Cypris fuscata* Sharpe 1897 (non Jurine 1820). Sharpe, 1897:442-443, pl. 43, fig. 5.*Cypris testudinaria* Sharpe 1897. Sharpe, 1897:444-445, pl. 44, figs. 1-4.*Cypris (Cypris) fuscata* (in part) Sharpe 1897 (non Jurine 1820). Sharpe, 1908:403-405, pl. 53, figs. 1, 2, 4, non 3.*Cypris (Cypris) fuscata* (in part as var. *minor* G. W. Müller 1900) Sharpe 1897 (non Jurine 1820). Sharpe, 1918:818, fig. 1278b, c, d, non a.*Eucypris affinis hirsuta* Furtos 1933 (non Fischer 1851). Furtos, 1933:450-451, pl. 2, figs. 9-11, 16.*Type Locality:* Germany.

*Description of the Female:* An ostracod of the genus *Cypricercus*. In side view (fig. 105), the shell appears subtriangular with the height considerably greater than one-half of the length. The greatest height lies anterior to the middle where the dorsal margin forms a rounding, obtuse angle. Both the anterior and posterior slopes of the dorsal margin are equally slanted and pass without interruption into the margins of the two ends. The anterior end is more widely rounded than the posterior. The ventral margin shows a slight sinuation. Viewed from above, the shell appears broadly elliptical with the greatest width in the center of the shell and more than one-half the length. The ends are somewhat obtusely rounded, neither being acutely pointed. The length of the shell varies, individuals occasionally being as small as 1.00 mm. or as large as 1.30 mm. The young of this species bears characteristic shell sculpturing regarding which Zaddach (1844) in his original description of *Cypris reticulata* says: "Superficies lineis reticulatis et quasi insculptis ornata est, colore olivaceo, maculis nigricantibus." The shell of the adult is not sculptured.

The swimming setae of the antennae extend beyond the ends of the terminal claws. The penultimate podomere of the antenna has a length only four and one-half times the width; the posterior distal seta (fig. 106-B) of the antepenultimate podomere has a spherical basal portion. The claw-like setae of the outer masticatory process of the maxilla are toothed. The ventral margin of the furcal ramus (fig. 107) has a length twenty-two times the least width of the ramus. The terminal claw is equal to one-half of the length of the ventral margin of the ramus. The distal end of the dorsal seta reaches beyond the base of the subterminal claw and the terminal seta is considerably longer than the dorsal one.

*Description of the Male:* A single male specimen assignable to this species was available for study. This specimen was in poor condition, having been preserved for over forty years as a part of the collection of material in the "Field Zoology" Laboratory at the University of Illinois. The shell (fig. 108) is very flexible and thin, being little calcified. The surface of the valves are covered with fine hairs. The general shape is similar to that of the female. The testes (fig. 108-A, P) may be seen readily through the surface of each valve. In addition to the part of the testis always found in the posterior part of each valve, there is in this species an extension in the form of whorls in the anterior one-half of each valve. The appendages of the male are similar to those of the female. The prehensile palps offer no specific distinction. The ductus ejaculatorius is elongated and cylindrical with more than thirty whorls of spines. The penis (fig. 109) has a substantial inner lobe with a broadly rounded distal end; the middle lobe is thin and falciform in shape with the distal point directed toward the inner edge of the penis. In the writer's single specimen, a thin very much reduced flap may be distinguished on the outer edge of the penis. Whether or not this is actually the rudiments of an outer lobe cannot be determined with certainty because of lack of material. Alm (1914:pl. 1, fig. 3) shows no such outer appendage. The size of the male as given by Alm (1914) is 1.1 mm. to 1.2 mm. in length and the dimensions given for *Cypris testudinaria* by Sharpe (1897) is 1.15 mm. in length, 0.74 mm. in height, and 0.65 mm. in width. The length of the individual in the present writer's collection exceeds slightly 1.3 mm. in length but since the shell is very flexible and has been much flattened and distorted in mounting, this size certainly far exceeds the actual length in the undamaged animal.

Males are seldom seen in most collections and seem, indeed, to be more common in the colder parts of the range of this species. Sharpe (1908) reported, under the designation *Cypris fuscata* var. *minor*, the males as common in the Chicago region. Alm (1914) mentions under the name *Eucypris affinis hirsuta* Fischer (*E. fuscata minor* G. W. Müller) the presence of males in Newfoundland, Greenland, and Siberia.

*Remarks:* *Cypricercus reticulatus* (Zaddach 1844) is a variable species which has caused considerable confusion in the literature as a result of the morphological variation between young and adult and male and female. Much confusion has also been occasioned by the inability of investigators to separate this species from closely related species because the minute details of structure used in the differentiation were until recently unknown or misunderstood.

It is unfortunate that the name delegated to the young of this species, *reticulatus*, by Zaddach (1844) has not been retained by recent writers

on this group. For a number of years it was thought to be a species separate from the adult described by Fischer in 1851 under the name *Cypris affinis*. Sharpe (1897) did not realize that he had the young and mature of the same species and so continued to designate them separately. The sparsity of collections which contain both young and mature individuals contributed to the inability of recognition of the young which are characterized by a shell sculpturing lacking in the adult. Since there is a single generation each year and the transition from the "reticulatus" to the "affinis" type appears to take place more or less simultaneously in individuals of a given population, young and mature individuals are seldom found in the same collection.

The present writer is certain that he has the *Cypris reticulata* described by Zaddach and he is also certain that it is the young of the *Cypris affinis* of Fischer. European writers as Sars (1928), Wagler (1937), and Klie (1938a) give *reticulatus* as an unquestioned synonym of *affinis*. These same writers, however, continue to use the name *affinis* in spite of the fact that *reticulatus* has priority and should be the valid designation for this species. Sars (1928) states his reason for not using the earlier name, *reticulata*, as follows: "The specific name *reticulata* proposed by Zaddach and assigned by some recent authors to this species must, I think, be wholly discarded, as only applying to immature specimens." Such neglect of the name *reticulata* is in direct contradiction to that part of the International Rules of Zoological Nomenclature which reads as follows: "ARTICLE 26. The Law of Priority obtains and consequently the oldest available name is retained: . . . (b) When any stage in the life history is named before the adult." Unfortunately then, *Cypricercus reticulatus* must replace *C. affinis* as the valid name for the species under consideration.

Besides separately naming the young and adult of *C. reticulatus*, Sharpe (1897) apparently also named the males, designating them as a new species, *Cypris testudinaria*. Even though there is much similarity between males and females, Sharpe seems not to have recognized the identity of his male specimens. The reason for establishing a new species for the males was probably that the males of the now designated *C. reticulatus* were unknown in the literature at the time of Sharpe. In fact, Sars recently (1928) reported the males as unknown in spite of the fact that Alm described males as early as 1914. The description given by Sharpe (1897) for *Cypris testudinaria* agrees favorably with the description of males given by Alm (1914) under the designation *Eucypris affinis hirsuta*. As far as the *Cypris testudinaria* of Sharpe is concerned, his description is evidently based entirely upon male specimens for he particularly stresses the nature of the ductus ejaculatorius (Sharpe, 1897) but nowhere refers to the females.

The designation *Cypris fuscata* which Sharpe (1897) used for the species under discussion was certainly an error on his part resulting apparently from the inavailability of good descriptions of the closely related European species belonging to the genus *Cypris*. At the time of Sharpe, the exact identification of many of the European species of the genus *Cypris* was in doubt and no two authors agreed on the valid name or the identity in many of the species.

While *Cypricercus fuscatus* and *C. reticulatus* are closely related, there are several differences in structure upon which differentiation between species can be based. These structures were undescribed in early literature but are now well known and may be applied toward straightening out the synonymy of *C. fuscatus* and *C. reticulatus*. A comparison of the morphological differences separating *C. fuscatus* and *C. reticulatus* is given in the "remarks" under the description of the former. In spite of the fact that Sharpe in 1897 did not mention most of the structures now used as a basis for separation of *C. fuscatus* and *C. reticulatus*, there are certain minor differences such as shell shape, the general shape of the furca, and the relative lengths of the setae and claws of the furca, which clearly indicate that many of Sharpe's figures (1897:pl. 43, fig. 5; 1908:pl. 53, figs. 1, 4; 1918:figs. 1278c, d) illustrating his *C. fuscatus* are drawn from species assignable to *C. reticulatus* rather than to *C. fuscatus*.

Other writers besides Sharpe have been confused over the proper designation of this species. Furtos (1933) was aware that Sharpe's *fuscata* of 1897 was not the true *fuscata* of Jurine, and yet she unfortunately adopted Alm's designation of this species, *Ecypris affinis hirsuta* (Fischer), rather than the more nearly correct *Cypricercus affinis* as used by Sars and other European writers. It is now generally known that Alm (1916) made an error in assigning *hirsuta* as a subspecies of *affinis* for the two forms differ specifically in many ways. Chief among these differences (Klie, 1938a; Sars, 1928) is the smooth nature of the claws of the outer masticatory process in *C. hirsuta* and the toothed condition in *C. affinis*. The individuals described by Furtos (1933) were characterized by having toothed claws on the outer masticatory process and so cannot belong to the species *C. hirsutus* (Fischer 1851) Sars 1928.

*Ecology:* *C. reticulatus* is typically a species of vernal ponds. Very rarely it may be found along the edge of pools in vernal streams where there remains decaying grass from the previous growing season. It is associated with live and dead grass and algae. There appears to be a single generation each year. The young appear in the prevernal season before the ice has completely disappeared. The juveniles are characterized

by a reticulated sculpturing on the shell and may be found not later than the last of April at the latitude of Urbana, Illinois. Beginning with the first of May, only individuals lacking the sculpturing and therefore considered to be approaching maturity may be found. The eggs survive the drying up of the pond during the serotinal season and hatch at the end of the haemal season. Such a life cycle is also shown by Alm (1916) for this species under the designation *Eucypris affinis hirsuta* in Europe.

*Distribution:* *Cypricercus reticulatus* is common throughout the Holarctic region. Under the designation *Eucypris affinis hirsuta*, Alm (1914) described it from the Arctic region of North America. Sharpe (1897) reported it under a variety of names from Illinois, chiefly from the east central part of the state. Later (1908) he reported it from the Chicago region. In the writer's collections are specimens taken in March, 1940, from a pond near Reelfoot Lake, Tennessee, by Mr. Robert Yapp. The writer has this species in a collection made by Mr. F. R. Cagle in Jackson County, Illinois. This material was given the present writer by Dr. Victor Sprague who received it from Mr. Cagle. The writer has collected individuals of *C. reticulatus* from the following counties in Illinois: Champaign, Piatt, Vermilion, and Woodford.

#### GENUS CYPRINOTUS BRADY 1885

Form of shell variable, greatest height equal to or greater than one-half the length. The dorsal margin may be evenly arched or may have an obtuse apex (fig. 110). Valves commonly unequal; either the right or left valve may be the longer. Margin of one valve ornamented with small tubercles along part or all of the free margin; the margin of the other valve smooth. Swimming setae of the antennae well developed. The outer masticatory process of the maxilla with two claw-like setae which may or may not be toothed. Furca (fig. 111) moderately developed, the dorsal seta commonly longer than the terminal seta and located close to the subterminal claw. The terminal claw of the furca is longer than one-half the length of the ventral margin of the furcal ramus. The genus *Cyprinotus* is practically cosmopolitan. Two species are known from Illinois.

#### KEY TO SPECIES OF THE GENUS CYPRINOTUS IN ILLINOIS

- a. Left valve of shell larger than the right valve; dorsal seta of furca with a length about equal to one and one-half times the length of the terminal seta (fig. 111).....*C. incongruens* (Ramdohr 1808) Turner 1895
- b. Left valve of shell smaller than the right valve; dorsal seta of the furca has a length equal to about twice the length of the terminal seta.....*C. pellucidus* Sharpe 1897

*Cyprinotus incongruens* (Ramdohr 1808) Turner 1895

(Pl. VIII, figs. 110, 111)

*Cypris incongruens* Ramdohr 1808. Ramdohr, 1808:86, pl. 3, figs. 1-12, 15, 18-20; Turner, 1893:8, pl. 2, figs. 17-21.

*Cyprinotus incongruens* (Ramdohr 1808) Turner 1895. Turner, 1895:330-331, pl. 68, figs. 9-16.

? *Cyprinotus pellucida* Sharpe 1897. Sharpe 1897:434-435, pl. 42, figs. 1-6.

*Cypris incongruens* Ramdohr 1808. Sharpe, 1908:405-406, pl. 54, figs. 1-3.

*Cypris (Cyprinotus) incongruens* Ramdohr 1808. Sharpe, 1918:815, fig. 1270a, b, c, d.

*Cyprinotus incongruens incongruens* (Ramdohr 1808) Turner 1895. Furtos, 1933: 447-449, pl. 4, figs. 8-12.

*Type Locality:* Europe.

*Description of the Female:* An ostracod of the genus *Cyprinotus*. In side view (fig. 110), the right shell is elongated, highest just posterior to the center, the greatest height being about three-fifths of the length. The dorsal margin is arched and often has a slight sinuation just anterior or posterior or both anterior and posterior to the apex in at least one of the valves. The ventral margin has a slight sinuation in the center. In a view from above, the left valve overlaps the right. The shell is widest at its posterior one-third; anterior more acutely pointed than the posterior. The greatest width is about eighty-five per cent of the greatest height. The anterior and the ventral-posterior margins of the right valve are ornamented with a row of tubercles. The margins of the left valve are smooth. The length of the shell of the adult varies from 1.4 to 1.75 mm. and the color varies from a yellow to a brownish-yellow.

The natatory setae of the antennae extend beyond the tips of the terminal claws; the claw-like setae of the outer masticatory process of the maxilla are toothed. The furca (fig. 111) is stout, slightly bowed, with the terminal claw having a length about one-half the length of the dorsal margin of the furcal ramus. The length of the ventral margin of the furca is about eleven times the least width of the furca. The terminal seta has a length about one-half to two-thirds the length of the subterminal claw of the furcal ramus; the dorsal seta has a length about one and one-half times the length of the terminal seta and is removed from the subterminal claw by a distance equal to little more than the least width of the ramus. The subterminal claw measures approximately two-thirds the length of the terminal one.

*Description of the Male (after Klie, 1938a):* The present writer has found no males in his collections from Illinois. In the shell of the male, the greatest height lies in the middle. The shell is smaller than that of the female, measuring usually about 1.2 mm. in length. The prehensile palps are dissimilar and unequal; the right palp has a heavy propodus and the dactylus is swollen, being falciform and tapering gradually to a

blunt distal point; the left palp has a dactylus which is recurved and slender, having an even width throughout about the distal two-thirds of its length. The penis has only two lobes; the inner lobe is short and has a wide subtruncate distal margin; the middle lobe which extends distally beyond the inner is triangular in shape and the blunt point is directed toward the inner margin of the penis. The males are not common in many localities.

*Remarks:* This species was first reported from North America by Turner who included with his description drawings (1893:pl. 2, figs. 17-21) sufficiently accurate to allow verification of his determination. G. W. Müller (1912) questions Turner's identification of this form as expressed by the latter in 1895. Turner's drawings in 1893 are much better than those in 1895 and certainly Müller was justified in his criticism of the 1895 determination.

There is a possibility that *C. pellucidus* Sharpe 1897 (Sharpe, 1897, 1903) may be a species based on immature individuals of *C. incongruens*. Sharpe's drawings of the shell of *C. pellucidus* never show the gonads indicative of a mature animal. A discussion of this possible synonymy is given under the "remarks" in the description of *C. pellucidus*.

*Ecology:* Sharpe (1918) gives the habitat of this common species as "temporary ponds and watering troughs." Furtos (1933) reports it from a rock-pool along the shore of Lake Erie in Ohio. It is the general consensus of opinion among European workers (Alm, 1916; Sars, 1928; *et al.*) that this species is found in puddles, ponds, and ditches. The present writer has taken it more times from running waters than he has from temporary ponds and ditches. Not only is this species found along the edge in grass and vegetation of shallow, quiet waters but it may be taken from masses of algae which hang in swiftly running water. The kind of bottom seems to have no significance as individuals may be found equally abundant over sand as over mud bottom. The writer's collections were made in the aestival season but whether or not this gives any information upon the seasonal occurrence may be doubted especially since Alm (1916) found this species abundant throughout most of the year in Sweden.

*Distribution:* *Cyprinotus incongruens* is cosmopolitan except that it has not been reported from Australia (Klie, 1926a). In North America, it was reported first from Ohio by Turner (1893) and then by Furtos (1933). Sharpe (1897) reported it from Florida and later (1908) from Pennsylvania. Alm (1914) found it in material from Greenland, and Dobbin (1941) has reported it from Oregon. The present writer has found it in collections from several counties in the northern one-half of Illinois. It has not been found in the southern part of the state.

*Cyprinotus pellucidus* Sharpe 1897

*Cyprinotus pellucida* Sharpe 1897. Sharpe, 1897:434-435, pl. 42, figs. 1-6.

*Cypris pellucida* (Sharpe 1897) Sharpe 1903. Sharpe, 1903:988-989, pl. 68, figs. 1-5; Weckel, 1914:178, figs. 7, 8.

*Cypris (Cyprinotus) pellucida* (Sharpe 1897) Sharpe 1903. Sharpe, 1918:815, figs. 1269a, b, c, d, e, f.

*Type Locality:* Illinois.

*Description of the Female (after Sharpe, 1897, 1903):* A species of the genus *Cyprinotus*. Shell from the side, nearly elliptical, elongate; dorsal margin evenly arched with the greatest height near the center. The ventral margin is nearly straight, but with a slight sinuation near the center. The anterior and posterior ends rounded, the posterior more broadly. In view from above, according to Sharpe's figures (1897:pl. 42, fig. 2; 1903:pl. 68, fig. 2), the left valve is slightly smaller than the right; the anterior end is rather acutely pointed, the posterior more blunt. However the text of Sharpe's description of 1903 reads as follows: "The right valve of shell is slightly smaller than the left, its anterior margins armed with a row of about twenty-five tuberculiform teeth. The margin of the left valve has a rather wide hyaline flange and a row of scattered tubercles along the inner margin." The size of individuals range from 1.1 mm. to 1.4 mm. long, 0.80 mm. high and 0.51 mm. wide.

The swimming setae of the antennae reach but little beyond the distal ends of the terminal claws. The claw-like setae of the outer masticatory process of the maxilla are toothed. The furca is stout, slightly bent, and about twice as long as the terminal claw. The subterminal claw is about three-fourths of the length of the terminal one. The dorsal seta has a length about equal to the length of the subterminal claw and is removed from the base of the subterminal claw by a distance less than the least width of the furcal ramus. The terminal seta is about one-half as long as the dorsal seta.

*Males:* Unknown.

*Remarks:* The present writer has found it impossible to determine exactly what Sharpe had when he described *Cyprinotus pellucida* (sic!) in 1897. The writer believes that Sharpe may have founded his species upon immature individuals since he does not show the ovaries in the drawings of the shell even though he states that the shell is very transparent. In almost every morphological detail, the descriptions given by Sharpe (1897, 1903, 1918) for this species checks accurately with immature individuals of *Cyprinotus incongruens*. It is, however, impossible to reconcile the shell differences in valve overlap in *C. incongruens* and *C. pellucidus*. In adult *C. incongruens* the left valve overlaps the right and the same condition is usually found in the young with the exception that in some young individuals the valves appear equal in size. Regard-

ing *C. pellucidus*, Sharpe (1903) states that the right valve is smaller than the left. In his drawings, however, in 1897, 1903, and 1918, the right valve is always shown as the larger. If the text of his 1903 description is correct and the left valve is larger than the right, then possibly *C. pellucidus* is a synonym of *C. incongruens*. On the other hand, if the left valve is consistently smaller than the right (as shown in the drawing by Weckel (1914, fig. 7)), then *C. pellucidus* must be retained as a valid species.

The unsatisfactory and uncertain manner in which the genus *Cyprinotus* was diagnosed in the first decade of the present century is shown by Sharpe transferring his species *pellucida* from the genus *Cyprinotus* to the genus *Cypris* in 1903. Part, at least, of this uncertainty was the result of several writers about 1900 attempting to characterize certain genera by the manner of propagation in the included species. Since the genus *Cyprinotus* was thought to contain only species whose individuals reproduced by syngamy, it was necessary to exclude the species *C. pellucidus* because males were and still are unknown. Later, this criterion was practically neglected and the genus *Cyprinotus* reconstructed along entirely morphological lines. Because the manner of reproduction varies in morphologically united groups of ostracods, it is not possible to use the manner of reproduction as a generic criterion.

*Ecology*: Sharpe (1897) reports this species from a roadside ditch and from a creek, as well as from an aquarium started with material from a creek. Later (1903) he reported it from a trough fed by a spring (Idaho).

*Distribution*: Sharpe (1897) described this species from material taken in Adams, Mason, and Champaign Counties, Illinois. Later, he (1918) gave the range of this species as Washington, Idaho, Illinois, and Mexico. The present writer has not rediscovered this species in Illinois.

## SUBFAMILY NOTODROMINAE

Distal podomere of the antenna long and slender; swimming setae extend far beyond the terminal claws. Outer masticatory process of the maxilla with six nearly equal, spine-like, toothed setae (fig. 113). Third thoracic leg with three unequally long setae. Ductus ejaculatorius with chitinous supporting rays not arranged in regular rows.

## KEY TO GENERA OF THE SUBFAMILY NOTODROMINAE IN ILLINOIS

- a. Antenna of six apparent podomeres; first thoracic leg without respiratory plate; distal three setae of third thoracic leg unmodified; terminal seta of the furca wanting (fig. 114).....Genus *NOTODROMAS* Lilljeborg 1853
- b. Antenna of five podomeres; first thoracic leg with a respiratory plate; setae on distal end of third thoracic leg modified for grasping; terminal seta of furca present.....Genus *CYPRIS* Zenker 1854

## GENUS NOTODROMAS LILLJEBORG 1853

Shell short with the height at least two-thirds of the length; dorsal margin forming an elevated arch; ventral surface flattened (fig. 112). Eyes well separated. The antenna with the penultimate podomere divided and so appearing to consist of six podomeres; the apparent distal podomeres long and slender, the swimming setae extending beyond the tips of the terminal claws. The respiratory plate of the first thoracic leg is lacking. The palps of the maxillae in the male are not similar; each is formed of two podomeres. Ultimate podomere of third thoracic leg small and with three almost equal setae. Furca with the terminal seta wanting; the dorsal seta very heavy and not far removed from the subterminal claw (fig. 114). A genus with few species: one from Sumatra, one from Ceylon, and one from the Holarctic region (Sars, 1928).

*Notodromas monacha* (O. F. Müller 1776) Lilljeborg 1853

(Pl. VIII, figs. 112-114)

*Cypris monacha* O. F. Müller 1776. O. F. Müller, 1776:199.*Notodromas monachus* (O. F. Müller 1776) Lilljeborg 1853. Lilljeborg, 1853:95-102, pl. 8, figs. 1-15; pl. 12, figs. 1, 2; pl. 25, fig. 16; Herrick, 1882:252.*Notodromas monacha* (O. F. Müller 1776) Lilljeborg 1853. Sharpe, 1908:417-419, pl. 59, figs. 1-8; Shelford, 1913:144, fig. 94; Sharpe, 1918:808, figs. 1255a, b, c, d, e.*Type Locality:* Europe.

*Description of the Female:* A species of the genus *Notodromas*. Shell with the greatest height about seven-tenths of the length; greatest height slightly posterior to the middle of the elevated dorsal margin. Posterior end more broadly rounded than the anterior; ventral margin nearly straight and produced posteriorly into a point beyond the posterior shell margin. From above, ovate with greatest width behind the middle and equal to two-thirds of the length. Length 1.1 mm.

The ultimate podomere of the antenna equal in length to the penultimate; the swimming setae of the antenna reach the tips of the single terminal claw. Furca curved, with the terminal claw greatly exceeding in length one-half of the ventral margin of the furca.

*Description of the Male:* Male with shell (fig. 112) larger than female; ventral margin bowed without a posterior tooth-like projection. Length of shell 1.2 mm. Appendages as in the female. Prehensile palps well developed and dissimilar; furca (fig. 114) more curved than in the female.

*Remarks:* A detailed description of *N. monacha* is not needed here since Sharpe in 1908 adequately described and figured this species from material taken in northwestern Indiana.

*Ecology:* *N. monacha* has been reported by Sharpe (1908) as living in "permanent bodies of pure fresh water which is also rich in aquatic vegetation." The single male individual of this species taken by the writer was collected from the shore of a lake where there was an abundance of aquatic plants. This species is rare as this single individual was found in one of more than seventy-five collections made by Mr. Bertrand A. Wright and by the writer at different times from the lakes in McHenry and Lake Counties, northwest of Chicago, Illinois.

*Distribution:* *N. monacha* has been reported from Minnesota by Herrick (1882) and from northern Indiana (near Chicago, Illinois) by Sharpe (1908) and Shelford (1913). Dobbin (1941) reports it from Alaska. The present writer's collection was made on June 29, 1940, from south of Waucanda, Lake County, Illinois. In general, this species is widely distributed throughout the Holarctic region.

#### GENUS CYPROIS ZENKER 1854

Shell from the side, short and high, greatest height about two-thirds of the length; ventral side of the shell not flattened. Eyes not widely separated. Antennae of five podomeres; the penultimate podomere not divided; the ultimate podomere small with several end claws. The swimming setae almost reach the tips of the end claws. Right and left prehensile palps of male differing little. First thoracic leg with a well developed respiratory plate. Ultimate podomere of the third leg small, being partially enclosed by the penultimate podomere. Distally, the third leg forms a seizing apparatus similar to that found in the members of the subfamily Cyprinae *s. str.*; with only two conspicuous distal setae, the third being reduced to a tooth-like structure. Furca with two claws and two setae. A single species is found in Illinois.

#### *Cyprois marginata* (Strauss 1821) Zenker 1854

*Cypris marginata* Strauss 1821. Strauss, 1821:59, pl. 1, figs. 20-22.

*Cyprois marginata* (Strauss 1821) Zenker 1854. Sharpe, 1908:415-416, pl. 58, figs. 1-5; Shelford, 1913:177, 179, 185, fig. 129; Sharpe, 1918:809, figs. 1256a, b, c, d.

*Type Locality:* Europe.

*Description of the Female (chiefly after Klie, 1938a):* An ostracod of the genus *Cyprois*. From the side, shell high in the middle, greatest height about seven-tenths of the length. Anterior margin evenly rounded; the posterior margin flatly rounded; and the ventral margin slightly sinuate. Seen from above, the right shell overlaps the left; the anterior is more pointed than the posterior; and the greatest width which is about

one-half of the length lies in the middle of the shell. Shell measures 1.7 mm. in length.

The penultimate podomere of the antenna narrow, terminal claws slender; swimming setae extending to the tip of the claws. Furcal ramus little curved; dorsal seta modified claw-like and subequal to the terminal claw.

*Description of the Male (after Sars, 1928):* Shell of male smaller than that of female. Shell similar to that of female except the posterior margin is more rounded. Prehensile palps nearly equal in shape and size. Furcal ramus much more curved in the male than in the female. Length of shell of male about 1.5 mm.

*Remarks:* Representatives of this species have not been collected by the present writer in Illinois. As a result, it is thought advisable to give only a brief synopsis of the specific description as complete descriptions may be found in both European and American works on ostracods (*vid.* Sharpe, 1908).

*Ecology:* Both Sharpe (1908) and Shelford (1913) report this species from vernal ponds.

*Distribution:* *Cyprois marginata* is found throughout most of the Holarctic region except Asia. Sharpe (1908) and Shelford (1913) found this species in the region of Jackson Park, Chicago, Illinois. Furtos (1933) found this species in Ohio.

## SUBFAMILY CYPRIDOPSINAE

Shell from the side, usually high and short (figs. 115, 118); from above, either tumid or compressed. Length of shell not over 1.0 mm. Antenna of five podomeres with swimming setae well developed or reduced. Outer masticatory process with two spine-like setae either toothed or smooth. Distal end of third thoracic leg modified for grasping (fig. 120). Furca reduced to a base ending distally in a long seta or "flagellum" (fig. 117). Reproduction in many species entirely parthenogenetic. The subfamily is cosmopolitan.

## KEY TO GENERA OF THE SUBFAMILY CYPRIDOPSINAE IN ILLINOIS

- a. Shell tumid, valves nearly equal; ultimate podomere of the maxillary palp cylindrical, longer than wide.....Genus *CYPRIDOPSIS* Brady 1867
- b. Shell compressed, right valve higher than the left and extending dorsally above the left; ultimate podomere of the maxillary palp distally wider than long (fig. 119).....Genus *POTAMOCYPRIS* Brady 1870

## GENUS CYPRIDOPSIS BRADY 1867

Shell short, high, tumid (fig. 115). Valves differ little, neither projects conspicuously above the other dorsally. Swimming setae of the antenna well developed. Terminal podomere of the maxillary palp cylindrical, not widened distally. The respiratory plate of the first thoracic leg carries two or more setae. Furca greatly reduced, consisting of a base tapering distally to form a long seta or "flagellum" with a second shorter seta attached to the posterior margin close to the distal end of the base (fig. 117). Members of this genus are found in nearly all parts of the world. A single species, *Cypridopsis vidua* (O. F. Müller 1776), known from Illinois.

*Cypridopsis vidua* (O. F. Müller, 1776) Brady 1867

(Pl. VIII, figs. 115-117)

*Cypris vidua* O. F. Müller 1776. O. F. Müller, 1776:199.

*Cypridopsis vidua* (O. F. Müller 1776) Brady 1867. Sharpe, 1897:469-470; Kofoid, 1908:258; Shelford, 1913:152, figs. 81a, b; Sharpe, 1918:807, fig. 1253.

*Cypridopsis vidua obesa* Furtos 1933 (*non* Brady and Robertson 1869). Furtos, 1933:431.

*Cypridopsis pustulosa* Furtos 1933. Furtos, 1933:431-432, pl. 6, figs. 5-9.

*Type Locality:* Europe.

*Description of the Female:* A species of the genus *Cypridopsis*. Shell (fig. 115) from the side: ovoid in shape; the greatest height just posterior to the center and about two-thirds of the length. Dorsal margin broadly arched, usually with a definite angulation at the highest point. Ventral margin slightly sinuated in most shells; anterior and posterior margins rounded, the anterior slightly more narrowly rounded than the posterior. The ventral surface is flattened. Seen from above: shell tumid; the greatest width is slightly posterior to the middle and little exceeds the greatest height. The anterior margin of the right valve (fig. 116) with fifteen to twenty tubercles which are inconspicuous in some individuals. The surface of the shell is marked by minute impressions. The surface is hairy. The shell is yellowish white to light green in color and usually is ornamented by four color bands which extend from the dorsal margin down the side of each valve. These bands vary in color from light green to dark green, to black in some individuals. There are usually four bands which are placed as follows: one along the posterior margin of the shell, one near the anterior margin, one immediately behind the eye, and one between the last mentioned and the posterior band. These blotches or bands vary considerably in intensity

and indeed may be too weak to be detected by reflected light. Such bands may be demonstrated on isolated valves by the use of transmitted light.

The swimming setae of the antennae extend beyond the ends of the terminal claws. The respiratory plate of the first thoracic leg bears five setae. The terminal seta or "flagellum" of the furca (fig. 117) about equals twice the length of the base. Average length of the shell is about 0.70 mm.

*Male:* Unknown. The report of males from middle Europe by Spandl (1925) is doubted by European workers (Klie, 1938a).

*Remarks:* *Cypridopsis vidua* is variable in shape, size, and color. The greatest variation is in the color bands, some individuals having dark conspicuous bands, others inconspicuous bands. The apparent absence of color bands has led many investigators to assign individuals to the species *C. obesa* Brady and Robertson 1869. Furtos (1933), for example, assigns certain individuals to *C. vidua obesa* Brady and Robertson 1869 in spite of the fact that she found no anatomical differences between the two forms, *vidua* and *obesa*, as they occur in Ohio. Since there are differences in shell shape and the number of setae on the respiratory plate of the first leg in *vidua* and *obesa* and these differences have been recognized by Sars (1928) and Klie (1938a), it is apparent that Furtos has erred in assigning the Ohio specimens with the anatomical characteristics of *vidua* to the group *obesa*. It is very doubtful if *Cypridopsis obesa* occurs in North America, as all illustrations of American individuals assigned to *obesa* are without doubt indistinctly banded individuals of *vidua*. The writer has found a great variation in color in single population samples; and, indeed, many shells, which appear to be without bands, are seen to have bands when cleared valves are examined by transmitted light.

The variability of the shell is demonstrated by the tubercles along the anterior margin of the right valve. This variation in size and number of tubercles has led to some confusion which has culminated in the creation by Furtos (1933) of a new species, *Cypridopsis pustulosa*, to include individuals which are unbanded and which have tubercles along the anterior margin of the right valve. Although most authors do not mention these tubercles, they are known to occur in *Cypridopsis vidua*, as Klie (1938a) states: "Der V. R. [Vorderrand] der r. Sch. [rechte Schale] weist an der Innenseite eine aus etwa 20 winzigen Höckerchen bestehende Körnelung auf." These tubercles are often inconspicuous but may nearly always be detected even when very minute by an examination under high magnification of isolated right valves which have been deeply stained in acid fuchsin and cleared. There appears to be no correlation between the intensity of the color bands and the prominence of the tu-

bercles. In fact, many shells showing deeply colored blotches distinctive of *vidua* also show pronounced tubercles (which Furtos gives as the chief characteristic of her species *pustulosa*) along the anterior margin of the right valve.

The cause of the variability in color is unknown. It is doubtful if it is the result of the development of populations differing in color. The present writer has noticed that individuals taken in late summer from masses of algae and aquatic vegetation are usually more darkly colored than are specimens taken earlier in the season before the green plants replace the dead vegetation left from the previous year. It is entirely possible that either through the action of additional sunlight or by the ingestion of more green plant material, the pigment may become more highly developed. Such an hypothesis would necessarily require verification experimentally.

*Ecology:* *Cypridopsis vidua* is the most common of all the ostracods in Illinois. It was taken by the present writer in 505 of the 713 collections made in Illinois. Not only is it found everywhere, but there are few ostracods which are found in such great numbers of individuals in single collections. It is especially abundant in permanent still waters although it will tolerate considerable current when aquatic vegetation is present as a substratum. It is found only to a limited extent in April and May, and for this reason is not often taken from early vernal ponds. *Cypridopsis vidua* is present in most collections made in June and July regardless of the habitat although they reach their greatest abundance in the algae and aquatic vegetation of permanent lakes, river backwaters, and vernal ponds which do not dry up until late in the serotinal season.

*Distribution:* This species is common throughout the Holarctic region and has been reported from the Neotropical as well (Klie, 1926a). In every county in Illinois in which the writer made a reasonable sampling, *Cypridopsis vidua* was present.

#### GENUS POTAMOCYPRIS BRADY 1870

Shell compressed; the right valve projects much beyond the left dorsally. Valves usually hairy (fig. 118). Swimming setae of the second antenna usually well developed (fig. 118-S); extending to the tips of the terminal claws or beyond. Terminal podomere of the maxillary palp short, distally wider than long, and armed with short claw-like setae (fig. 119). The respiratory plate of the first thoracic leg with not more than two setae.

Only one species, *P. smaragdina* (Vávra 1891), known from Illinois.

*Potamocypris smaragdina* (Vávra 1891) Daday 1900

(Pl. VIII, figs. 118-124)

*Cypridopsis smaragdina* Vávra 1891. Vávra, 1891:80-81, fig. 26; Sharpe, 1897:470-471, pl. 48, figs. 11-12.*Potamocypris smaragdina* (Vávra 1891) Daday 1900. Sharpe, 1903:992, pl. 65, figs. 5-7; 1918:808, figs. 1254a, b, c.*Potamocypris smaragdina* (Vávra 1891) var. *compressa* Furtos 1933. Furtos, 1933: 435-436, pl. 6, figs. 10-14; Dobbin, 1941:231-232, pl. 2, figs. 1-6.*Type Locality:* Bohemia.

*Description of the Female:* A species belonging to the genus *Potamocypris*. Shell (fig. 118) from the side with a high rounding dorsal margin, giving the shell a three-sided appearance. The greatest height is little more than one-half the length; greatest height behind the eye but anterior to the middle of the dorsal margin. Posterior end pointed and narrower than the anterior. The margins of the two ends merge into the dorsal margin without any interruption. The ventral margin is slightly sinuated. The right valve extends above the left dorsally; the left shell extends beyond the right by its hyaline flange both anteriorly and posteriorly. This flange is confined posteriorly to the posterior-ventral corner and intensifies the acutely pointed appearance; anteriorly it extends from a little below the eye along the anterior margin of the shell and ends near the anterior end of the ventral margin. Considerable variation is shown in the extensiveness of the development of this flange. From above, the shell appears elliptical, bluntly pointed posteriorly, more acutely pointed anteriorly; the greatest width is less than one-half the length and located in front of or near the middle. Surface of shell hirsute; the hairs are stout and almost spine-like, directed posteriorly parallel to each other. They are appressed closely to the shell surface. The valve surfaces are pitted. The color varies but is usually light green or yellowish-green and commonly displays two dorsal lateral blotches of some shade of green. Length and height of valves of several females from Illinois (mounted in diaphane and measured to include the flanges) are as follows:

RIGHT		LEFT	
Length	Height	Length	Height
0.64 mm.	0.39 mm.	0.66 mm.	0.38 mm.
0.62	0.36	0.64	0.35
0.63	0.37	0.66	0.38
0.56	0.36	0.58	0.36

The swimming setae of the antennae extend beyond the ends of the terminal claws by one-third of their own length which is about equal to the length of the claws. The base of the furca narrows rapidly to form the "flagellum."

*Description of the Male:* The shell of the male differs somewhat

from the female in size and shape. On the whole, the (fig. 121) shell is much more elongate, the height little more than one-half of the length; the peak of the dorsal margin more attenuated than in the female. The anterior and posterior slopes of the dorsal margin are also more flattened. The ventral margin is conspicuously sinuated; the hyaline margin of the anterior end is well developed. The coloration, sculpturing, and hirsuteness of the shell similar to the female. The testes extend in the form of a whorl to the anterior one-half of the shell (fig. 121-A). The soft parts are like those of the female.

Measurements of the shell halves of several mature males (mounted in diaphane; measurements include the hyaline border or flange (fig. 121-F)) are as follows:

RIGHT		LEFT	
Length	Height	Length	Height
0.52 mm.	0.28 mm.	0.58 mm.	0.32 mm.
0.52	0.28	0.55	0.29
0.56	0.32	0.61	0.33

The right prehensile palp (fig. 122b) has a long cylindrical propodus with two stout setae near the distal end of the anterior margin; the dactylus is narrow and gently curved. The left prehensile palp (fig. 122a) is larger than the right, the propodus is stout and has two small lateral setae near the distal end of the anterior margin. The dactylus is stout, falciform, and is acutely pointed with a small protuberance near the point. The ductus ejaculatorius (fig. 123) is elongated with thirteen to fifteen rows of chitinous spines. The penis (fig. 124) has a wide base and a single lateral lobe. The lateral lobe is distally bilobed, stout, and extends beyond the blunt end of the base.

Males were present in six of fifty collections selected at random. They appear to be equal in number to the females in the collections in which they occur. There seems to be no correlation between the presence of males and the season or locality in which they occur.

*Remarks:* *Potamocypris smaragdina* is extremely variable in size, shape, and color of shell. This variability, along with the mistakes in the original description as given by Vávra (1891), has led to some misconception regarding this species. In assigning Illinois material to *P. smaragdina*, Sharpe (1897) remarks that the eye in Illinois material is below and anterior to the highest point of the shell in contrast to the condition in the type material of which Vávra (1891) wrote: "Die Schale ist fast dreiseitig, im ersten Drittel, über dem durch die Schale durchschimmernden Auge am höchsten." If a straightedge is laid along the dorsal margin parallel to the ventral margin of the shell in Vávra's drawing (1891:81, fig. 26 (1)), it will be found that the highest point

of the shell is distinctly posterior to the eye much as it is in Illinois specimens.

Furtos (1933) seems also to have been led astray by Vávra's incomplete and erroneous description of the type material. She bases the separation of her variety *compressa* from the type of Vávra on two differences: (1) the Ohio form is longer, lower, and narrower than the European, and (2) the swimming setae of the antennae in the Ohio form extends beyond the terminal claws by the length of the claws rather than "beyond the terminal claws by only one-third the length of the claws" (Furtos, 1933) as in the European form. Both of these differences may be obliterated when Vávra's description is properly understood. In the first place, the height, 0.48 mm., given by Vávra (1891) is plainly an error. If the shell figured (Vávra, 1891:fig. 26 (1)) is measured and the height computed from the height-length ratio (assuming the length to be 0.68 mm.) the height will be about 0.38 mm. Thus the height is little more than one-half the length. This is verified by Wagler (1937). The height of the variety *compressa* as given by Furtos then coincides with this computed height for *P. smaragdina* of Europe. The error in the height given in Vávra's work is apparently a typographical error. Such errors are very common in Vávra's work on the ostracods of Bohemia and several others occur in Vávra's description of *P. smaragdina*. Regarding the difference in length of the swimming setae of the antennae as given by Furtos, there has been a misunderstanding in the reading of Vávra's description. From the nature of his sentence structure, it is impossible to tell whether he intended to say that the swimming setae extend beyond the end claws of the antenna by one-third of the length of the setae or one-third of the length of claws, for he (1891) writes: "Von den übrigen Arten [*Cypridopsis villosa*] unterscheidet sie sich hauptsächlich durch die Bildung des zweiten Antennenpaares, dessen am Ende des dritten Gliedes inserierte Schwimmborsten sehr lang sind, so dass sie das Ende der Klauen um ein drittel ihrer Länge überragen." Furtos (1933) took this to mean that the setae extend beyond the claws by one-third of the length of the claws. However, that Vávra meant that the setae extend beyond the end claws by one-third of the length of the setae is supported by Wagler (1937) who writes: "Schwimmb. [Schwimmborsten] der Ant. [Antenne] überragen die Endkl. [Endklaue] um  $\frac{1}{3}$  ihrer eigenen Lg. [Länge]." Thus there remains no difference between the var. *compressa* of Furtos and the typical European form except a slightly smaller width in the former. This difference can probably be assigned to individual variation.

*Ecology:* *Potamocypris smaragdina* is a common species especially of permanent waters. Only twenty of the one hundred and eighteen collections made by the writer containing this species were from tempo-

rary still and running waters, the others from permanent waters, about one-half from lakes and one-half from streams. The reason for not finding this species in temporary waters may be its seasonal appearance for it seldom becomes abundant before late May when many of the temporary waters have become dry. This species usually reproduces parthenogenetically but a number of males do occur in many collections.

*Distribution:* This species is found in North America and in Bohemia and Switzerland in Europe. The writer has taken it from all parts of the state of Illinois although it is much more abundant in the northern two-thirds than in the southern one-third of the state.

### FAMILY DARWINULIDAE

Surface of shell smooth; hinge without teeth. Antennule composed of six podomeres, with strong spine-like setae. Antenna with a base of two podomeres and an endopodite of three podomeres, also a vestigial exopodite armed with two setae. Swimming setae lacking. Mandible with a short palp of three podomeres; of which the first is wide and has a row of long feathered setae. The respiratory plate of the mandible is small and is armed with short setae. The masticatory processes of the maxilla are short and heavy; the palp has two podomeres, the basal one wide, the distal one small and relatively narrow. The respiratory plate of the maxilla well developed, very large, with numerous large feathered setae. the first thoracic leg with a strong masticatory structure; a leg-like palp of three podomeres, and a circular respiratory plate with numerous setae. The second and third thoracic legs are similar, each composed of five podomeres and adapted for crawling. The furca is completely lacking, the body ending posteriorly in a short, unpaired cone-like projection (fig. 126). The ovaries do not originate in the cavity between the shell plates; the female carries the eggs in the posterior dorsal part of the shell cavity during their development. A single genus is known.

### GENUS DARWINULA BRADY AND NORMAN 1889

With characteristics of the family Darwinulidae.

Of the few species known, only one, *Darwinula stevensoni*, has been reported from North America.

#### *Darwinula stevensoni* (Brady and Robertson 1870)

Brady and Norman 1889

(Pl. IX, figs. 125, 126)

*Argilloecia* (?) *aurea* Brady and Robertson 1870. Brady and Robertson, 1870:16, pl. 8, figs. 4-5.

*Polycheles stevensoni* Brady and Robertson 1870. Brady and Robertson, 1870:25-26, pl. 7, figs. 1-7; pl. 10, figs. 4-14.

*Darwinula stevensoni* (Brady and Robertson 1870) Brady and Norman 1889. Brady and Norman, 1889:122-123, pl. 10, figs. 7-13; pl. 13, figs. 1-9; pl. 23, fig. 5.

*Darwinula improvisa* Turner 1895. Turner, 1895:336-337, pl. 81, figs. 1-3, 13.

*Darwinula stevensoni* (Brady and Robertson 1870) Brady and Norman 1889. Sharpe, 1918:807, fig. 1252.

*Type Locality:* British Isles.

*Description of Female:* An ostracod of the genus *Darwinula*. From the side, the shell (fig. 125) very narrowly wedge-shaped with the broader end posterior. The greatest height equal to about two-fifths of the length and highest near the middle of the posterior one-half of the shell. The dorsal margin is very flatly arched; the ventral margin is straight. Viewed from above, the shell appears elongate; the greatest width lies at the posterior one-third and is greater than one-third of the length; posterior end rounded, anterior end pointed. The right shell extends beyond the margins of the left both anteriorly and posteriorly. Each of the nine muscle scars are wedge-shaped and together form a rosette in the posterior part of the anterior one-half of the shell. The shell measures about 0.70 mm. in length. The distal podomere of the mandibular palp is several times longer than wide.

*Males:* The present writer has seen no males of this species. There are no available descriptions of males; the extent of reports in the literature regarding the nature of the male is a single drawing of the penis by Brady and Robertson (1870:pl. 10, fig. 13).

*Remarks:* G. W. Müller (1912) in "Das Tierreich" lists this species under the designation *D. aurea* (Brady and Robertson 1870). Brady and Robertson described this species twice in the same publication, first under the specific designation *aurea* (1870) and then under *stevensoni* (1870). Since there is no statement in the International Rules of Nomenclature which would require the recognition of the first (according to the pagination) of two names given in a publication, the name *stevensoni* rather than *aurea* should be retained for this species because: (1) in *stevensoni* the description is based on several individuals while the description of *aurea* is based on a single individual; (2) the description and figures of *stevensoni* are more complete than those for *aurea*; (3) the designation *stevensoni* was preferred by Brady in the work by Brady and Norman (1889) and *aurea* is given as a synonym; (4) *stevensoni* is a long established name and is used by most writers.

*Ecology:* *D. stevensoni* appears to be an inhabitant chiefly of large lakes. Turner (1895) reported it under the name *D. improvisa* from a sandy bottom reservoir about three miles in circumference. The present writer secured a single individual in material taken from the sandy bottom

of a large lake of glacial origin. That it is not always associated with a sandy bottom is shown by Sars (1928) who found it on a muddy bottom. This species usually reproduces parthenogenetically.

*Distribution:* *D. stevensoni* is nearly Holarctic in distribution, having been reported from Europe and North America. In North America, it was reported by Turner (1895) from Atlanta, Georgia. The present writer found a single female in a collection made by Bertrand A. Wright on August 8, 1940 from Hastings Lake near Antioch, Lake County, Illinois.

### FAMILY CYTHERIDAE

Shell variable in shape and sculpturing; seldom smooth, usually with reticulations; often with spines, furrows, or tubercles (fig. 127). Valves nearly equal; often tooth-like projections along the hinge (fig. 137-AT, PT). The antennules consist of a base of two podomeres and an endopodite of three or four podomeres. The setae of the antennules are short and stout, often claw-like. The exopodite or the flagellum" (fig. 131-F) of the antenna is represented by a long hollow seta forming a duct carrying the secretion from a gland which is thought to furnish adhesive material used by the animal in crawling over smooth surfaces. The endopodite of the antenna is composed of three podomeres; the long penultimate one may be divided. Swimming setae lacking. Three pairs of thoracic legs similar and all adapted for crawling. Furca always greatly reduced (fig. 138). In the male, the penis is always present and well developed (figs. 134, 141); the ductus ejaculatorius is absent; and a male accessory sense organ consisting of numerous setae on a short base (fig. 135) is located between and somewhat medially to the bases of the first and second pairs of thoracic legs. The gonads do not lie between the plates of the valves but are in the body lateral to the intestine. In some species, the eggs are retained in the shell cavity during development.

The family includes over thirty genera belonging to several subfamilies, most of which are marine. Two subfamilies, Limnocytherinae and Entocytherinae, are known from the fresh-waters of North America.

### KEY TO SUBFAMILIES OF THE CYTHERIDAE IN ILLINOIS

- a. Free margins of valves flattened, with many long pore-canals (fig. 128-P); shell usually subrectangular, often with protuberances or furrows (fig. 127); the respiratory plate of the mandible well developed; the furca usually with two short setae (fig. 132).....Subfamily LIMNOCYTHERINAE
- b. Free margins of the valves without conspicuous pore-canals; shell usually reniform or subelliptical and without furrows or protuberances; respiratory plate of mandible usually reduced to two or three setae; the furca extremely rudimentary.....Subfamily ENTOCYTHERINAE

## SUBFAMILY LIMNOCYTHERINAE

Shell weakly calcified. Margin of each valve with many pore-canals (fig. 128-P). Eyes fused. Both antennules and antennae foot-like and adapted for creeping. Exopodite (flagellum) (fig. 131-F) of the antenna well developed in both sexes. Palp of the mandible of three podomeres and with a well developed respiratory plate. Furca small, usually with two short spine-like setae (fig. 138). The members of this subfamily are entirely fresh-water in habitat. A single genus, *Limnocythere*, is known from Illinois.

## GENUS LIMNOCYTHERE BRADY 1867

Shell thin, usually with either protuberances or furrows (fig. 127-F, P) or both; the free margin edge where the valves meet is extremely wide with long, slender, often branching pore-canals (fig. 127-M). Endopodite of the antennules consist of three podomeres, of which the distal one is four times longer than wide and is armed with four setae of which two are fused at their bases (fig. 130-F). Antenna with three terminal claws; the exopodite (flagellum) is divided into basal and distal portions by an articulation (fig. 131-A). Respiratory plate of the mandible with five long apical and two short lateral setae. The palp of the maxilla has a distinct distal podomere with one of the distal setae claw-like. The thoracic legs are similar and each has two setae on the anterior margin of the proximal podomere (fig. 139). Furca cone-shaped with one terminal seta and one lateral seta (fig. 132). Three species belonging to this genus are known from Illinois.

In the literature there is some confusion regarding the proper spelling of the name of this genus. Some writers as Sharpe (1897) and Sars (1928) give the spelling as "*Limnocythere*." Most writers, on the other hand, give the spelling as "*Limnocythere*." The latter is correct. It was used by Brady in a publication dated September, 1867. The spelling wherein an "i" replaces the "o" results from certain writers following a later publication by Brady (1868). The content of this later publication was read before the Linnean Society of London in May, 1866. Since reading a paper does not constitute publication, the more orthographically correct name, *Limnocythere*, stands as the valid designation for this genus.

## KEY TO SPECIES OF THE GENUS LIMNOCYTHERE IN ILLINOIS

- 1a. Shell with conspicuous, well developed protuberances (fig. 127-P); anterior margin of shell with tubercles (fig. 128-T); dorsal seta of furca arising from a papilla (fig. 132-P).....*L. verrucosa* sp. nov.
- b. Shell without well developed protuberances (fig. 140); anterior margin of shell without tubercles; dorsal seta of furca arises directly from the base without the intervention of a papilla (fig. 138-D).....2

- 2a. Shell with two dorsal-lateral furrows (fig. 140); surface sculpturing conspicuous; furca blunt, with one of the setae at the distal end (fig. 138) ..... *L. reticulata* Sharpe 1897
- b. Shell with one dorsal-lateral furrow; surface sculpturing inconspicuous; furca with base tapering to an acute point and both of the setae well removed from the distal end..... *L. illinoisensis* Sharpe 1897

*Limnocythere verrucosa* sp. nov.

(Pl. IX, figs. 127-135)

*Type Locality:* West Loon Lake, Lake County, Illinois.

*Description of the Female:* A species of the genus *Limnocythere*. From the side: shell (fig. 127) subrectangular; height slightly more than one-half the length; dorsal margin straight; ventral margin well sinuated near the center; anterior margin evenly rounded with a very wide hyaline border; posterior margin with an angulation near the center. Teeth of the hinge weak. Four oval muscle scars with the longitudinal axis of each scar parallel to the dorsal margin of the shell (fig. 127-S); the four scars forming a row with the axis of the row at right angles to the axis of each individual scar. The scars are subcentrally placed. The shell bears laterally and dorsally in the anterior one-half two furrows (fig. 127-F). These are similar to the furrows in *L. reticulata*. Near the furrows there are two large, rounded protuberances. One of these is anterior and ventral to the anterior furrow; the other is posterior and slightly ventral to the posterior furrow. A third large protuberance is located very near the ventral margin of each valve just posterior of the deepest portion of the sinuation. The flattened, hyaline border (fig. 128) of the shell contains numerous pore-canals near the outer ends of which originate large setae. Between these setae the outer margin is plumose, the hairs being closely placed and delicate. The anterior margin also has eight to twelve small tubercles along its edge. The entire shell including the hyaline borders is sculptured with small raised areas giving the shell a reticulated appearance. From above, the shell (fig. 129) appears moderately inflated as a result of the protuberances. The width is nearly equal to the height, being but slightly more than one-half of the length.

The length and height of several right valves are as follows (mounted in diaphane; measurement includes the hyaline border):

<i>Length</i>	<i>Height</i>
0.55 mm.	0.30 mm. (holotype)
0.56	0.30
0.54	0.30
0.60	0.30

The antennules are stout; the length of the ultimate podomere is five and one-half to six times the width. The two subdistal claws are

relatively short, subequal or equal to the ultimate podomere, and the tips are on a level with the point of fusion of the two terminal setae. The two terminal setae (fig. 130-F) are fused basally for a distance equal to the length of the terminal podomere of the appendage. Of the unfused ends of these two setae, the more slender one has a free portion which is three times the length of the unfused portion of the stouter of the pair. The "flagellum" (fig. 131-F) of the antenna reaches somewhat past the center of the longest terminal claw. The terminal claws of the thoracic legs are relatively short in comparison to those of most *Limnocythere*; the claw of the first leg is equal to the sum of the last two podomeres of the appendage; the claw of the second leg is about one and one-third times the sum of the lengths of the last two podomeres; and the claw of the third thoracic leg has a length little more than the sum of the distal three podomeres.

The furca (fig. 132) is peculiar in having a trilobed base; the middle lobe is conical with a small needle-like seta on the blunt apex; the posterior lobe (fig. 132-P) is small, papilla-like, and bears a long seta which reaches to the distal end of the terminal lobe.

*Description of the Male:* The shell (fig. 133) of the male differs from that of the female in being slightly longer and not relatively as high and by having the protuberances greatly reduced. The shell is prominently inflated directly above the ventral sinuation. The length and height of the right valves of two male shells are as follows (mounted in diaphane; the margins included in the measurements):

<i>Length</i>	<i>Height</i>
0.59 mm.	0.28 mm.
0.62	0.27

In the male, the sculpturing of the shell and the nature of the margins are similar to those of the female. The appendages also differ little from those of the female. The ultimate podomere of the antennule is slightly more slender, and the "flagellum" of the antenna reaches nearly to the tips of the end claws. The terminal claw of the third leg is equal at least to seven-eighths of the length of the rest of the leg.

The base of the penis (fig. 134) has an irregularly curved anterior margin. There are several appendages. One is L-shaped and is directed posteriorly; a second large appendage passes along the base of the penis and is directed anteriorly along the outside. It extends slightly beyond the base anteriorly. Other smaller appendages and chitinous supporting rods are present. The furca is very different from that of the female but such differences are not unusual in species of this genus. The furca is a tapering cone, very long and bearing two setae, one near the base and another near the sharply pointed tip. The furca looks much like that of *L. illinoisensis* Sharpe 1897 (Sharpe, 1897:pl. 39, fig. 12).

*Remarks:* *Limnocythere verrucosa* sp. nov. is markedly different from other Illinois species of *Limnocythere*. The most readily available criterion for recognition is the peculiar inflated condition of the shell caused by the bulging protuberances. The furca of the female differs from all other species of *Limnocythere* by having the posterior seta elevated on a papilla.

*Ecology:* This species has been taken only from permanent lakes in which there is an abundance of aquatic vegetation or alga.

*Distribution:* *L. verrucosa* was collected for the writer by Bertrand A. Wright from West Loon Lake, Lake County, Illinois, on August 7, 1940. No other records are known.

The holotype (female) and allotype (male) of this species are deposited in the U. S. National Museum (Cat. Nos. 81085 and 81086). Paratypes of both sexes are in the collections of Dr. H. J. Van Cleave and the writer.

*Limnocythere reticulata* Sharpe 1897

(Pl. IX, fig. 136-141)

*Limnocythere reticulata* Sharpe 1897. Sharpe, 1897:423-425, pl. 39, figs. 1-7; 1918: 806, figs. 1250a, b, c.

non *Limnocythere reticulata* Procter 1933. Procter, 1933:231, figs. 39a-d.

*Type Locality:* Urbana, Illinois.

*Description of the Female:* An ostracod of the genus *Limnocythere*. From the side, shell (fig. 136) appears subrectangular; dorsal margin straight; ventral margin with a sinuation; anterior and posterior margins evenly rounded. The height is but little more than one-half of the length. From above, the shell is elliptical with the sides slightly flattened and the anterior end narrowly and acutely pointed. The greatest width is little more than one-third of the length and lies posterior to the middle of the shell. Each valve has two lateral furrows in the vicinity of the eye. The surface is sculptured with a network of polygonal reticulations which cover the surface except in the region of the eye. The four muscle scars are arranged in a transverse row; each scar is elliptical in shape and lies with its long axis parallel to the longitudinal axis of the other scars and to the dorsal margin of the shell. The length of the shell is 0.65 to 0.70 mm. Length and height of right valves of several female shells from Illinois are given as follows (mounted in diaphane and measured to include the hyaline border):

<i>Length</i>	<i>Height</i>
0.66 mm.	0.36 mm.
0.68	0.38
0.63	0.32
0.70	0.36

The antennules have a narrow ultimate podomere about seven times as long as wide and are armed distally with four setae, two of which have their bases fused. Of these two, one has the free portion about twice as long as the free portion of the other. The antenna has three terminal spines, the two longer ones are equal and have a length equivalent to four times the length of the ultimate podomere. The third claw measures about seven-eighths the length of the longer ones. The terminal claw of the first thoracic leg is a little longer than the sum of the lengths of the last two podomeres; terminal claw of the third leg very long, equal to the sum of the last three and one-half podomeres. The furca (fig. 138) is described by Sharpe (1897) as follows: "Rudimentary caudal rami cylindrical, thick, blunt, about three times as long as wide, with a small seta near base, not over two thirds as long as the width of the ramus, and a stouter one near the tip of the ramus, twice as long as the preceding one."

*Description of the Male:* The shell (fig. 140) of the male differs considerably from the female by being longer, relatively less high, and with the posterior end more narrowly rounded and obtusely pointed. Measurements of the right valves (borders included) of the shells of several males from Illinois are as follows (mounted in diaphane):

<i>Length</i>	<i>Height</i>
0.74 mm.	0.34 mm.
0.76	0.38
0.78	0.40
0.72	0.36

The appendages are similar to those of the female except that the terminal setae of the third leg (fig. 139) is much longer, the length being equal at least to the length of the rest of the leg. The penis (fig. 141) is large; the anterior margin is irregularly rounded; the base ends bluntly in a point. Several appendages are present of which the largest is falciform and extends posteriorly beyond the base.

*Remarks:* This species is readily distinguishable from other Illinois species of *Limnocythere* by its reticulated shell surface and its lack of protuberances. The blunt, short furca with the terminal seta near the rounded distal end is an important diagnostic characteristic.

The record of this species by Procter (1933) from Lake Wood on Mount Desert Island, Maine, appears to be based on an erroneous specific determination. The shell pictured (Procter, 1933:figs. 39a, b) is certainly not the *reticulata* of Sharpe since it is too elongate and the dorsal margin is not straight. Likewise the illustration of the penis (his fig. 39d) lacks the prominent appendage characteristic of the penis of *L. reticulata* Sharpe.

*Ecology:* *Limnocythere reticulata* is a species from running waters although it may be found on occasion in temporary pools. It is seldom found in permanent lakes. It tolerates all conditions of current in streams since it does not swim but creeps along the bottom or over the vegetation. In the writer's seventy collections of this species, all were taken in May and June except one in July and one in August.

*Distribution:* *Limnocythere reticulata* is known only from Illinois. Sharpe (1897) collected the type material from a pond near Urbana, Champaign County, Illinois. The present writer has taken this species from twenty-five counties scattered chiefly over the central and southern parts of the state.

*Limnocythere illinoisensis* Sharpe 1897

*Limnocythere illinoisensis* Sharpe 1897. Sharpe, 1897:425-428, pl. 39, figs. 8-13; pl. 40, figs. 1-6; Kofoid, 1908:258; Sharpe, 1918:807, figs. 1251a, b, c, d, e.

*Type Locality:* Havana, Illinois.

*Description of the Female (after Sharpe, 1897):* A species of the genus *Limnocythere*. From the side, subelliptical with dorsal margin straight, both ends evenly rounded, and the ventral margin with a deep sinuation at the anterior one-third just below the muscle scars. The greatest height of the shell is less than one-half of the length; the posterior part of the shell has a greater height than the anterior part. From above, the shell is pointed anteriorly; convex posteriorly; the sides are nearly parallel and straight. There is a single lateral furrow; the shell reticulations are faint. The dimensions of the shell as given by Sharpe are: length, 0.88 mm.; height, 0.40 mm.; width, 0.29 mm.

The terminal podomere of the antennule is four times as long as wide. Terminal claw of second leg is nearly equal in length to the sum of the lengths of the distal three podomeres of the appendage. "Rudimentary caudal rami cylindrical, six to seven times as long as wide, gradually tapering to a seta-like extremity which is five sevenths as long as the main part of the ramus. Two dorsal setae: one situated about the width of the ramus from base and as long as the width of the ramus; the other just anterior to the seta-like termination, and about the same length as the first" (Sharpe, 1897).

*Description of the Male (after Sharpe, 1897):* The male is much like the female except for details of some of the appendages. The ultimate podomere of the antennule is five times as long as wide, the terminal claw of the antenna has three or four strong teeth near the tip. The claw of the second leg has two or three accessory teeth near the tip; the claw of the third leg is very long, as long as the lengths of the podomeres of the leg united. This claw has cross-striations on the distal one-half.

Sharpe gives no verbal description of the male copulatory organs and it is impossible to describe them adequately from his figure (Sharpe, 1897:pl. 40, fig. 2).

*Remarks:* The present writer has not observed individuals of this species in any of his collections.

*Ecology:* Sharpe's specimens were from lakes connected with the Illinois River. Here the bottom was sandy. His collection of type material was in May. Kofoed (1908) found this species during the months of March, August, and November.

*Distribution:* The only known records of this species are those of Sharpe (1897) and Kofoed (1908) regarding material taken mostly from the Illinois River and connected lakes near Havana, Illinois.

#### SUBFAMILY ENTOCYTHERINAE

The subfamily Entocytherinae is represented in Illinois by two species of the genus *Entocythere*, *E. illinoisensis* Hoff 1942 and *E. copiosa* Hoff 1942. For descriptions of these two species, the reader is referred to the writer's recent review of the subfamily Entocytherinae (Hoff, 1942).

## SUMMARY

(1) The ostracods of Illinois, and the entire United States as well, have received relatively little attention. Sharpe (1897, 1903, 1908, 1910) investigated the ostracod fauna of Illinois but his work is relatively incomplete since he confined his collecting of material chiefly to Champaign, Mason, and Cook Counties. He gives little comprehensive information on the ecology of the group in any of his publications.

(2) During the course of this investigation, the present writer traveled nearly five thousand miles in the spring and summer of 1940. Over seven hundred collections of ostracods were made from sixty-six counties of the state. At the time of making each collection, the available ecological data were recorded for future analysis.

(3) The writer found that the ostracod species of Illinois may be separated into four groups according to habitat: (a) temporary running waters as vernal streams; (b) temporary still waters as vernal ponds; (c) permanent still waters as large lakes and the backwaters of rivers; and (d) permanent running waters. While many species are typically found in one of these four habitats, others fall into more than one group.

(4) An attempt was made to analyze the field data to find what factors control the habitat range and distribution of ostracod species. It was found that distribution is not correlated with the type of bottom but that there is a distinct relationship between the amount of current in a habitat and the presence of certain species of ostracods. The hydrogen ion concentration apparently has some effect upon distribution by inhibiting certain species from extending their range to the southern part of the state where the waters are often acid. Two species of *Cypria* are able to tolerate acid conditions.

(5) Ostracods do not enter into immutable association either with other species of ostracods or species of plants found in the habitat. In studying lakes, it is found that the same species of ostracods may be found in all parts of a lake regardless of the kind of vegetation.

(6) Reproduction is both parthenogenetic and syngamic in some species of ostracods, in other species one or the other of the types of reproduction may predominate in varying degree. A list is given showing the kind of reproduction in Illinois species as indicated by the relative abundance of males.

(7) A short summary is given of the distribution of species of ostracods living in Illinois both in relation to world-wide and state range. Seventeen species are reported for the first time from Illinois. One family, Darwinulidae, represented by a single species is reported for the first time from the state.

(8) A complete discussion is given of the external morphology of the

fresh-water ostracods as an aid to future study and specific determination. A summary is given of the morphology of various physiological systems.

(9) A discussion is given of the larger categories in the classification of the order Ostracoda with a comparison of the systems devised by various authors.

(10) In the systematic portion of the thesis, descriptions are given of the thirty-nine free-living ostracod species reported from Illinois. Of these, eleven are reported as being new to the literature. Of these new species, ten belong to the family Cypridae and one belongs to the family Cytheridae.

(11) Keys are given as an aid in the determination to species of the free-living ostracods known to occur in Illinois.

## BIBLIOGRAPHY

The following bibliographical list contains all the known references to the ostracods of Illinois and in addition most publications relative to the fresh-water Ostracoda of North America. Literature concerned with ostracods exotic to North America is usually cited only when reference is made thereto in the text.

Publications indicated by the asterisk (\*) have not been reviewed by the writer. All of these are early writings which have little taxonomic significance except as the descriptions have been expanded and completed by more recent workers.

ALLEN, S. A.

1933. Parasites and commensals of North Carolina crayfishes. *J. Elisha Mitch. Sci. Soc.*, 49:119-121.

ALM, GUNNAR

1914. Beiträge zur Kenntnis der nördlichen und arktischen Ostracodenfauna. *Ark. Zool.*, 9(5):1-20.  
1916. Monographie der Schwedischen Süßwasser-Ostracoden nebst systematischen Besprechungen der Tribus Podocopa. *Zool. Bidr. Uppsala*, 4:1-248.

BERGOLD, ALFRED

1910. Beiträge zur Kenntnis des innern Baues der Süßwasserosttracoden. *Zool. Jb. Anat.*, 30:1-42.

BERNECKER, A.

1909. Zur Histologie der Respirationsorgane bei Crustaceen. *Zool. Jb. Anat.*, 27:583-630.

BLAKE, CHARLES H.

1931. Two freshwater ostracods from North America. *Bull. Mus. Comp. Zool. Harvard*, 72:279-292.

BRADY, G. S.

- \*1864. On species of Ostracoda new to Britain. *Ann. Mag. Nat. Hist.*, Ser. III, 13:59-64.  
1867. A synopsis of the recent British Ostracoda. *Intell. Observ.*, 12:110-130.  
1868. A monograph of the recent British Ostracoda. *Trans. Linn. Soc. London*, 26:353-495.  
\*1870. Notes on Entomostraca taken chiefly in the Northumberland and Durham District. *Nat. Hist. Trans. Northumb.*, 3:361-373.  
1885. Notes on Entomostraca collected by Mr. A. Haly in Ceylon. *J. Linn. Soc. London*, 19:293-317.

BRADY, G. S., and NORMAN, A. M.

1889. Monograph of the marine and freshwater Ostracoda of the North Atlantic and of North-western Europe. 1. Podocopa. *Trans. R. Dublin Soc.*, Ser. II, 4:61-270.

BRADY, G. S., and ROBERTSON, D.

1870. The Ostracoda and Foraminifera of tidal rivers. *Ann. Mag. Nat. Hist.*, Ser. IV, 6:1-33.

BREHM, V.

1932. Vorläufige Mitteilungen über die Süßwasserfauna Neuseelands. *Zool. Anz.*, 99:79-81.  
1939. Zur Entomostrakenfauna der südlichen Halbkugel. *Zool. Anz.*, 126:33-40.

BRUES, CHARLES T.

1932. Further studies on the fauna of North American hot springs. *Proc. Amer. Ac. Sci. Boston*, 67:185-303.

CHAMBERS, V. T.

1877. New Entomostraca from Colorado. *Bull. U. S. Geol. Geog. Sur. Terr.*, 3:151-155.

CLAUS, C.

1872. Beiträge zur Kenntniss der Ostracoden, I. Entwicklungsgeschichte von Cypris. *Schr. Ges. Naturw. Marburg*, 9:151-166. (Also published separately in 1868).

1892. Beiträge zur Kenntniss der Süsswasser-Ostracoden, I. Arb. zool. Inst. Wien, 10:147-216.
1895. Beiträge zur Kenntniss der Süsswasser-Ostracoden, II. Arb. zool. Inst. Wien, 11:17-48.
- COCKERELL, T. D. A.  
1912. The fauna of Boulder County, Colorado, II. Univ. Colorado Stud., 9:41-52.
- CREASER, EDWIN P.  
1931. Some cohabitants of burrowing crawfish. Ecology, 12:243-244.
- CUSHMAN, JOSEPH A.  
1905. A new ostracod from Nantucket. Amer. Natural., 39:791-793.  
1907. Ostracoda from southeastern Massachusetts. Amer. Natural., 41:35-39.  
1908. Fresh-water crustacea from Labrador and Newfoundland. Proc. U. S. Mus., 33:705-714.
- DADAY, E. VON  
\*1900. Ostracoda Hungariae. Budapest.  
1905. Untersuchungen über die Süsswasser-Mikrofauna Paraguays. Zoologica (Stuttgart), 44:1-374.
- DANA, JAMES D.  
1852. United States Exploring Expedition during the years 1837-1842 under the command of Ch. Wilkes. Vol. 13. Crustacea. Part 2. Cypridae. Philadelphia.
- DOBBIN, CATHERINE N.  
1941. Fresh-water Ostracoda from Washington and other western localities. Univ. Wash. Pub. Biology, 4:174-246.
- DODDS, GIDEON S.  
1908. A list of the Entomostraca of Colorado. Univ. Colorado Stud., 5:243-250.
- EDDY, SAMUEL  
1934. A study of fresh-water plankton communities. Illinois Biol. Mono., 12(4):1-93.
- FASSBINDER, K.  
1912. Beiträge zur Kenntnis der Süsswasserostacoden. Zool. Jb. Anat., 32: 533-576.
- FISCHER, S.  
\*1851. Über das Genus Cypris und dessen bei Petersburg vorkommende Arten. Mem. savants sci. St. Petersburg, 7:127-167.  
1855. Beitrag zur Kenntniss der Ostracoden. Abh. der Akad. Munchen Mathem.-Physikal. Cl., 7:637-666.
- FORBES, S. A.  
1888. Studies of the food of fresh-water fishes. Bull. Illinois Lab. Nat. Hist., 2:433-538.  
1893. A preliminary report on the aquatic invertebrate fauna of the Yellowstone National Park, Wyoming, and of the Flathead Region of Montana. Bull. U. S. Fish Comm. 1891, 11:207-258.
- FOWLER, HENRY W.  
1912. The Crustacea of New Jersey. Ann. Rep. New Jersey Mus., 1911:29-651.
- FURTOS, NORMA C.  
1933. The Ostracoda of Ohio. Ohio Biol. Sur., 5:411-524.  
1935. Fresh-water Ostracoda from Massachusetts. J. Washington Ac. Sci., 25:530-544.  
1936a. Fresh-water Ostracoda from Florida and North Carolina. Amer. Mid. Natural., 17:491-522.  
1936b. On the ostracods from the Cenotes of Yucatan and vicinity. Carnegie Inst. Washington, pub. no. 457:89-115.
- GALTISOFF, PAUL S.  
1937. General methods of collecting, maintaining, and rearing marine invertebrates in the laboratory. Culture methods for invertebrate animals. Comstock Publishing Co., Ithaca, N. Y. Pages 5-40.

- HALDEMAN, S. S.  
 1841. (Descriptions of new Cypris species). Proc. Ac. Nat. Sci. Philad., 1:53.  
 1842a. (Descriptions of new Cypris species). Proc. Ac. Nat. Sci. Philad., 1:166.  
 1842b. (Description of a new Cypris species). Proc. Ac. Nat. Sci. Philad., 1:184.
- HANSTRÖM, B.  
 1924. Beitrag zur Kenntnis des zentralen Nervensystems der Ostracoden und Copepoden. Zool. Anz., 61:31-38.
- HERRICK, C. L.  
 1879. Microscopic Entomostraca, Ann. Rep. Geol. Nat. Hist. Sur. Minnesota, 7:81-123.  
 1882. On Notodromas and Cambarus. Ann. Rep. Geol. Nat. Hist. Sur. Minnesota, 10:252-254.  
 1887. Contribution to the fauna of the Gulf of Mexico and the South. Mem. Denison Sci. Assoc., 1(1):1-56.
- HIRSCHMANN, N.  
 1912. Beitrag zur Kenntnis der Ostrakodenfauna des Finnischen Meerbusens. Acta Soc. Fauna Flora Fennica, 36(2):1-66.
- HOFF, C. CLAYTON  
 1942. The subfamily Entocytherinae, a new subfamily of fresh-water Cytherid Ostracoda, with descriptions of two new species of the genus Entocythere. Amer. Mid. Nat., 27:63-73.
- JOHANSEN, FRITZ  
 1921. The larger freshwater crustacea from Canada and Alaska. Canad. Field-Natural., 35:88-94.
- JURINE, LOUIS  
 \*1820. Historie des Monocles, qui se trouvent aux environs de Genève. Genève.
- KAUFMANN, A.  
 1900a. Cypriden und Darwinuliden der Schweiz. Rev. Suisse Zool., 8:209-423.  
 1900b. Zur Systematik der Cypriden. Mitt. naturf. Ges. Bern, 103-109.
- KIEFER, F., and KLIE, W.  
 1927. Zur Kenntnis der Entomostraken von Brunnengewässern. Zool. Anz., 71:5-14.
- KLIE, W.  
 1925. Muschelkrebse als Baumhöhlenbewohner. Arch. Hydrobiol., 15:509-511.  
 1926a. Ostracoda. Biologie der Tiere Deutschlands, 22:1-56.  
 1926b. Über eine neue Art der Ostracodengattung Candona. Zool. Anz., 66:302-306.  
 1930. Ostracoden aus dem paraguayischen Teile des Gran-Chaco. Arch. Hydrobiol., 22:221-258.  
 1931a. Campagne spéologique de C. Bolivar et R. Jeannel dans l'Amérique du Nord (1928). Crustacés Ostracodes. Arch. Zool. exp. gén., 71:333-344.  
 1931b. Zwei neue Arten der Ostracoden-Gattung Candona aus unterirdischen Gewässern im südöstlichen Europa. Zool. Anz., 96:161-168.  
 1934. Zwei neue subterrane Ostracoden der Gattung Candona. Zool. Anz., 106:193-199.  
 1935. Drei neue Hölenostracoden aus der Umgebung von Laibach. Zool. Anz., 111:189-198.  
 1936. Neue Candoninae aus dem Grundwasser von Belgien. Bull. Mus. Hist. nat. Belg., 12(13):1-13.  
 1938a. Ostracoda, Muschelkrebse. Die Tierwelt Deutschlands und der Angrenzenden Meeresteile, etc., 34:i-iv, 1-230.  
 1938b. Ostracoden aus unterirdischen Gewässern in Süditalien. Zool. Anz., 123:148-155.  
 1938c. *Candona bilobata*, ein neuen Muschelkrebs aus dem Grundwasser der unteren Mainteles. Zool. Anz., 124:216-220.  
 1938d. Ostracoden aus dem Grundwasser der oberrheinischen Tiefebene. Arch. Naturg., new series, 7:1-28.

- KLUGH, A. B.  
 1927. The ecology, food-relations and culture of fresh-water Entomostraca. Trans. R. Canad. Inst., 16:15-99.
- KOCH, C. L.  
 \*1837-1841. Deutschlands Crustaceen, Myriopoden und Archniden. Heft 10, 11, 12 (1837); Heft 21 (1838); Heft 36 (1841).
- KOFOID, C. A.  
 1908. Plankton studies. V. The plankton of the Illinois River, 1894-1899. Part II. Constituent organisms and their seasonal distribution. Bull. Illinois Lab. Nat. Hist., 8:1-361.
- LILLJEBORG (LILJEBORG), WILH.  
 1853. De Crustaceis ex ordinibus tribus: Cladocera, Ostracoda et Copepoda, in Scania occurrentibus. Lund. i-xv, 1-223.
- MARSHALL, W. S.  
 1903. *Entocythere cambaria nov. gen. et nov. spec.*, a parasitic ostracod. Trans. Wisconsin Ac. Sci., 14:117-144.
- MÜLLER, G. W.  
 1900. Deutschlands Süsswasser-Ostracoden. Zoologica (Stuttgart), 30:1-112.  
 1912. Ostracoda. Das Tierreich, 31:i-xxxiii, 1-434. (Complete consideration of all literature prior to Dec. 31, 1908).  
 1927. Ostracoda. Kükenthal-Krumbach Handbuch der Zoologie, 3(1):399-434.
- MÜLLER, O. F.  
 \*1776. Zool. Danicae Prodomus. Havniae.  
 \*1785. Entomostraca seu Insecta testacea, quae in aquis Daniae et Norvegiae reperit, descripsit et iconibus illustravit. Lipsiae et Hawniae.
- MÜLLER-CALÉ, K.  
 1913. Über die Entwicklung von *Cypris incongruens*. Zool. Jb. Anat., 36:113-170.
- NEEDHAM, JAMES G., and LLOYD, J. T.  
 1930. The life of inland waters. Thomas, Springfield, Illinois. 1-438.
- NEEDHAM, P. R.  
 1938. Trout streams. Comstock, Ithaca. i-x, 1-233.
- NORDQVIST, O.  
 1885. Beitrag zur Kenntniss der inneren männlichen Geschlechtsorgane der Cypriden. Acta Soc. Sci. Fenn., 15:1-41.
- NOWIKOFF, M.  
 1908. Über den Bau des Medianauges der Ostracoden. Z. wiss. Zool., 91:81-92.
- PEARSE, A. S.  
 1910. A preliminary list of the crustacea of Michigan. Rep. Michigan Ac. Sci., 12:68-76.  
 1914. Report on the crustacea collected by the Walker-Newcomb Expedition in Northeastern Nevada in 1912. Occ. Pap. Mus. Michigan, 3:1-4.
- PROCTER, WILLIAM  
 1933. Biological survey of the Mount Desert Region. Pt. V. Marine fauna. Wistar Institute of Anatomy and Biology, Philadelphia. 1-402.
- RAMDOHR, K. A.  
 \*1808. Über die Gattung *Cypris* Müll. und drei zu derselben gehörige neue Arten. Mag. Ges. Fr. Berlin, 2:83-93.
- RAWSON, DONALD S.  
 1928. Preliminary studies of the bottom fauna of Lake Simcoe, Ontario. Univ. Toronto Stud. Biol., 31:75-102.  
 1930. The bottom fauna of Lake Simcoe and its role in the ecology of the lake. Univ. Toronto Stud. Biol., 34:1-183.

## SARS, G. O.

1890. Oversigt af Norges Crustaceer, med foreløbige Bemærkninger over de nye eller mindre bekendte Arter. Forh. Selsk. Christian., (1):1-80.
1895. On some South-African Entomostraca raised from dried mud. Christian. Selsk. Skr. I. Math.-nat. Kl., (8):1-56.
1896. On some West Australian Entomostraca raised from dried sand. Arch. Math. Naturv., 19(1):1-35.
1901. Contributions to the knowledge of the fresh-water Entomostraca of South America as shown by hatching from dried material. Arch. Math. Naturv., 24(1):1-52.
1926. Freshwater Ostracoda from Canada and Alaska. Report of the Canadian Arctic Expedition, 1913-1918, 7(1):1-22.
1928. An account of the Crustacea of Norway. Bergen, 9:i-xii, 1-277.

## SCHLEIP, W.

1909. Vergleichende Untersuchung der Eireifung bei parthenogenetisch und bei geschlechtlich sich fortpflanzenden Ostracoden. Arch. Zellforsch., 2:390-431.

## SCHMALZ, J.

1912. Zur Kenntnis der Spermatogenese der Ostracoden. Arch. Zellforsch., 8:407-441.

## SCHREIBER, E.

1922. Beiträge zur Kenntnis der Morphologie, Entwicklung und Lebensweise der Süßwasser-Ostracoden. Zool. Jb. Anat., 43:485-538.

## SHANTZ, H. L.

1907. A biological study of the lakes of the Pike's Peak region—preliminary report. Trans. Amer. Micr. Soc., 27:75-97.

## SHARPE, R. W.

1897. Contribution to a knowledge of the North American fresh-water Ostracoda included in the families Cytheridae and Cyprididae. Bull. Illinois Lab. Nat. Hist., 4:414-482.
1903. Report on the fresh-water Ostracoda of the United States National Museum, including a revision of the subfamilies and genera of the family Cyprididae. Proc. U. S. Mus., 26:969-1001.
1908. Further report on the Ostracoda of the United States National Museum. Proc. U. S. Mus., 35:399-430.
1910. On some Ostracoda, mostly new, in the collection of the United States National Museum. Proc. U. S. Mus., 38:335-341.
1918. The Ostracoda. Ward and Whipple: Fresh-water Biology, 790-827.

## SHELFORD, V. E.

1913. Animal communities in temperate America. University of Chicago Press. i-xiii, 1-368. (Second impression, 1937).

## SKOGBERG, TAGE

1920. Studies on marine Ostracods. Part I. Cypridinids, Halocyprids and Polycypids. Zool. Bidr. Uppsala, suppl., 1:1-784.

## SPANDL, HERMAN

1925. Die Tierwelt vorübergehenden Gewässer Mitteleuropas. Arch. Hydrobiol., 16:74-132.

## STORCH, O.

1926. Über den Fangapparat eines Ostrakoden. Verh. Dtsch. Zool. Ges., 2nd suppl., 80-85.
1933. Morphologie und Physiologie des Fangapparates eines Ostrakoden (*Notodromas monacha*). I, II, and III. Biol. Gen., 9(1):151-198; 355-394; (2):299-330.

## STRAUSS, HERCULE E.

- \*1821. Mémoire sur les Cypris de la classe des Crustacés. Mem. Mus. Hist. nat., 7:33-61.

## TURNER, C. H.

1892. Notes upon the Cladocera, Copepoda, Ostracoda and Rotifera of Cincinnati, with descriptions of new species. Bull. Sci. Lab. Denison Univ., 6:57-74.
1893. Additional notes on the Cladocera and Ostracoda of Cincinnati, Ohio. Bull. Sci. Lab. Denison Univ., 8(1):1-18.
1894. Notes on American Ostracoda, with descriptions of new species. Bull. Sci. Lab. Denison Univ., 8(2):13-26.
1895. Fresh-water Ostracoda of the United States. Second Rep. State Zool. Minnesota, 1895:277-337. (Contains a very extensive bibliography).
1896. Morphology of the nervous system of Cypris. J. Comp. Neurol., 6:20-44.
- 1899a. A male *Erpetocypris barbatus* Forbes. Zool. Bull., Boston, 2:199-202.
- 1899b. Synopsis of North-American invertebrates. V. Fresh-water Ostracoda. Amer. Natural., 33:877-888.

## UNDERWOOD, LUCIEN M.

1886. List of the described species of fresh water crustacea from America, north of Mexico. Bull. Illinois Lab. Nat. Hist., 2:323-386.

## VÁVRA, V.

1891. Monographie der Ostracoden Böhmens. Arch. naturw. Landesdf. Böhmen, 8(3):i-iv, 1-116. (Contains a comprehensive bibliography).
1897. Die Süsswasser-Ostracoden Deutsch-Ost-Africas. Tierwelt Deutsch-Ostafrika. Wiss. Forsch. über Land und Leute uns. Ost-Afrik, 4:1-28.

## WAGLER, ERICH

1937. Crustacea. Die Tierwelt Mitteleuropas, 2(2a):1-224.

## WARD, HELEN L.

1940. Studies on the life history of *Neoechinorhynchus cylindricus* (Van Cleave, 1913) (Acanthocephala). Trans. Amer. Micr. Soc., 59:327-347.

## WECKEL, ADA L.

1914. Free-swimming fresh-water Entomostraca of North America. Trans. Amer. Micr. Soc., 33:164-203.

## WEISMANN, AUGUST

1880. Parthenogenese bei den Ostracoden. Zool. Anz., 3:82-84.

## WELCH, PAUL S.

1935. Limnology. McGraw-Hill, New York. i-xiv, 1-471.

## WILLIAMS, LEONARD W.

1907. A list of the Rhode Island Copepoda, Phyllopoda, and Ostracoda with new species of Copepoda. 37th Ann. Rep. Comm. Fish. Rhode Island (special paper no. 30), 69-79.

## WOHLGEMUTH, R.

1914. Beobachtungen und Untersuchungen über die Biologie der Süsswasser-ostracoden; ihr Vorkommen in Sachsen und Böhmen, ihre Lebensweise und ihre Fortpflanzung. Int. Rev. Hydrobiol., Biol. Supp., 6:1-72.

## WOLF, J. P.

1919. Die Ostracoden der Umgebung von Basel. Arch. Naturg., Abt. A, 85(3):1-100.

## WOLTERECK, R.

1898. Zur Bildung und Entwicklung des Ostrakoden-Eies. Z. wiss. Zool., 64:596-623.

## ZADDACH, E. G.

1844. Synopseos Crustaceorum Prussicorum Prodromus. Dissertatio zoologica. Regiomonti (Königsberg).

## ZENKER, W.

1854. Monographie der Ostracoden. Arch. Naturg., 20(1):1-87.

## EXPLANATION OF PLATES

All drawings are from material collected in Illinois. A camera lucida was used in every instance and, unless otherwise indicated, all drawings are made from material mounted in diaphane and examined by transmitted light.

## PLATE I

*Cypricercus reticulatus* (Zaddach 1844) Sars 1928; female.

FIG. 1.—Animal with the left valve removed to show the appendages of the left side *in situ*. Scale: 0.5 mm.

AN—Antenna	P—Palp of mandible
AU—Antennule	SH—Edge of right valve
E—Eye	S—Sensory organ of antenna
F—Furca	X—Maxilla
FB—Food balls	R—First thoracic leg
G—Female genital lobe	L—Second thoracic leg
M—Mandible	T—Third thoracic leg
N—Natatory or swimming setae of antennule	V—Natatory or swimming setae of antenna

*Candona punctata* Furtos 1933; female.

FIG. 2.—Outside view of the right valve. Scale: 0.5 mm.

FIG. 3.—Second thoracic leg. Scale: 0.1 mm. E—End claw. S—Second podomere.

FIG. 4.—Third thoracic leg. Scale: 0.1 mm. C—Shorter companion distal seta of the similarly directed pair. P—Third or penultimate podomere.

FIG. 5.—Furca and genital lobe. Scale: 0.1 mm. D—Dorsal seta. G—Genital lobe.

*Candona fluviatilis* sp. nov.; female.

FIG. 6.—View from inside of right valve. Scale: 0.25 mm.

FIG. 7.—Shell sculpturing and muscle scars. M—Muscle scars (isolated ones not indicated by letter). S—Sculpturing.

FIG. 8.—View from outside of right antenna. Scale: 0.1 mm. S—Sensory organ.

FIG. 9.—First thoracic leg of right side. Scale: 0.1 mm. R—Setae representing the respiratory plate.

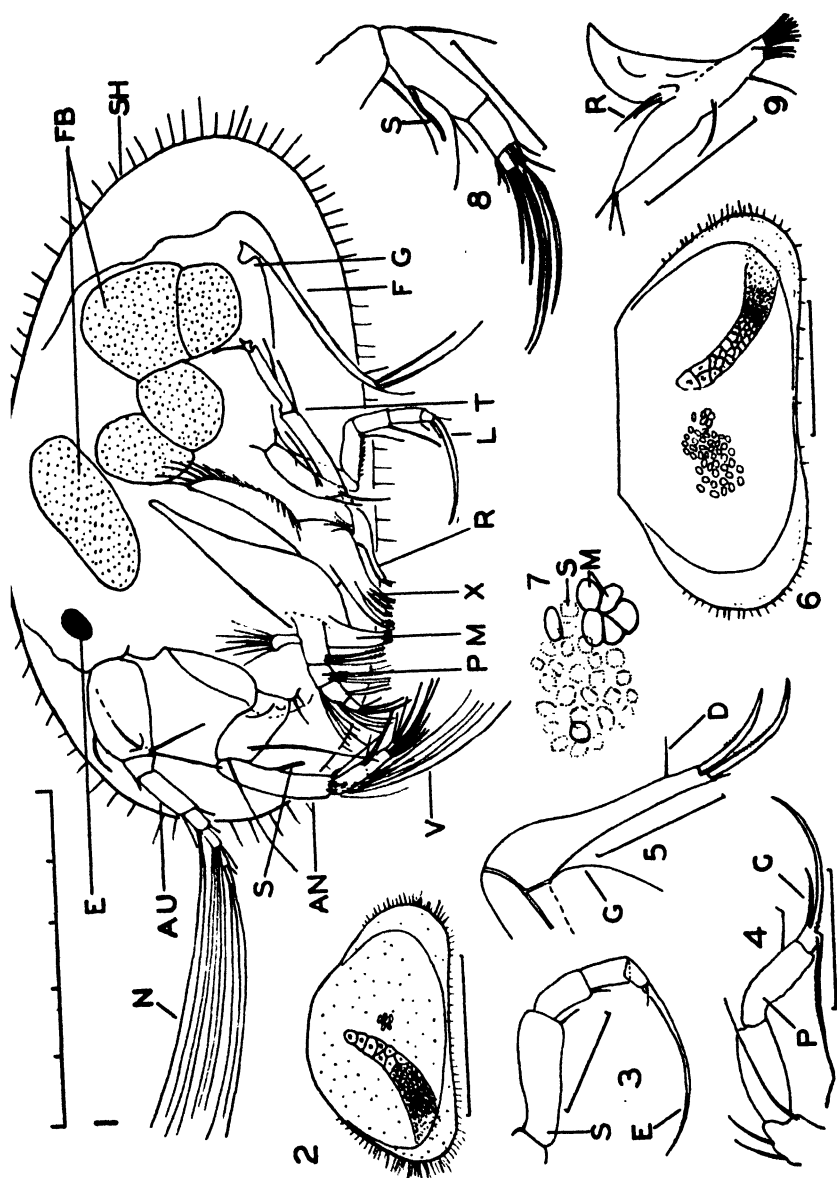


PLATE I

## PLATE II

*Candona fluviatilis* sp. nov.; female.

FIG. 10.—Third thoracic leg. Scale: 0.05 mm. P—Penultimate podomere showing undivided condition. S—Second podomere.

FIG. 11.—Furca and female genital lobe. Scale: 0.1 mm.

G—Genital lobe

T—Terminal claw

P—Dorsal seta

V—Terminal seta

S—Subterminal claw

*Candona simpsoni* Sharpe 1897; female.

FIG. 12.—Outline drawings of the shells of several specimens. Scale: 0.5 mm.

FIG. 13.—Third thoracic leg showing a combination of characters of the "simpsoni" form (as the spines on the margins of the antepenultimate and penultimate podomeres) and the "exilis" form (as the curved tip of the shortest distal claw). Scale: 0.1 mm.

FIG. 14.—Furca showing an S-shaped subterminal claw. Scale: 0.1 mm. S—Subterminal claw.

FIG. 15.—Furca showing a nearly straight subterminal claw, the dorsal thoracic seta, and the genital lobe. Scale as in fig. 14. D—Dorsal thoracic seta. G—Genital lobe.

FIG. 16.—Furca showing straight and slender claws. Scale as in fig. 14.

FIG. 17.—Furca of an immature individual just before the molt in which the third thoracic leg appears. The terminal seta of the furca is not developed. Scale: 0.05 mm. T—Terminal claw.

*Candona albicans* Brady 1864.

FIG. 18.—View from outside of the right valve of female. Scale as in fig. 21. O—Ovary.

FIG. 19.—End of the third thoracic leg of a female. Scale: 0.1 mm. P—Divided penultimate podomere.

FIG. 20.—Furca of female. Scale: 0.1 mm.

FIG. 21.—Inside view of the right valve of male. Scale: 0.5 mm. T—Testis.

FIG. 22.—Prehensile palps of male; (a) outside view of left palp; (b) inside view of right palp. Scale: 0.025 mm.

FIG. 23.—Penis. Scale: 0.1 mm.

*Candona biangulata* sp. nov.; female.

FIG. 24.—Inside view of the right valve (holotype). Scale: 0.25 mm.

FIG. 25.—Mandibular palp. Scale: 0.05 mm. B—Group of seta of antepenultimate podomere. F—Basal podomere of palp or the second podomere of the protopodite.

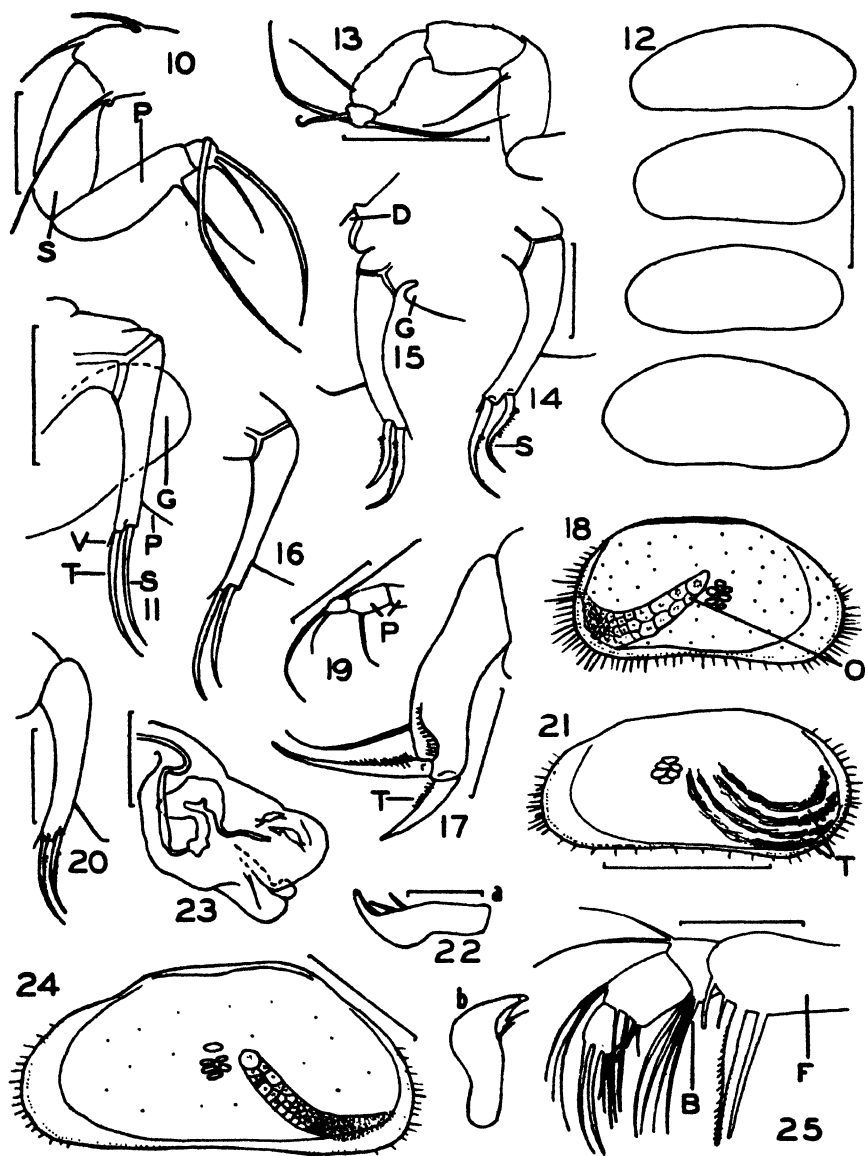


PLATE II

## PLATE III

*Candona biangulata* sp. nov.; female.

FIG. 26.—Second thoracic leg (mounted in glycerine). Scale: 0.1 mm. A—Second podomere. C—Distal claw. P—Penultimate podomere. U—Ultimate or fifth podomere.

FIG. 27.—Third thoracic leg (holotype). Scale: 0.5 mm.

FIG. 28.—Furca and genital lobe (holotype). Scale: 0.1 mm. G—Genital lobe.

*Candona distincta* Furtos 1933; female.

FIG. 29.—Outside view of left valve. Scale: 0.5 mm.

FIG. 30.—Furca and genital lobe. Scale: 0.1 mm. G—Genital lobe.

*Candona crogmaniana* Turner 1894; female.

FIG. 31.—Inside view of right valve. Scale as in fig. 33.

FIG. 32.—Base of furcal ramus and genital lobe. Scale: 0.1 mm. G—Genital lobe.

*Candona caudata* Kaufmann 1900; female.

FIG. 33.—Inside view of left valve. Scale: 0.25 mm.

FIG. 34.—Distal portion of the third thoracic leg showing divided penultimate podomere. Scale: 0.1 mm. P—Setae of similarly directed pair.

FIG. 35.—Furca and genital lobe. Scale: 0.2 mm.

*Candona sigmoides* Sharpe 1897.

FIG. 36.—Outside view of left valve of female. Scale: 0.5 mm.

FIG. 37.—Furca and genital lobe of female. Scale: 0.2 mm.

B—Base or ramus of furca

G—Genital lobe

C—Subterminal claw

S—Terminal seta

D—Dorsal seta

T—Terminal claw

FIG. 38.—Penis (mounted in glycerine). Scale: 0.2 mm.

*Candona indigena* sp. nov.

FIG. 39.—Lateral view of female from the left side (holotype; in alcohol). Scale as in fig. 36. S—Swimming setae of antennules.

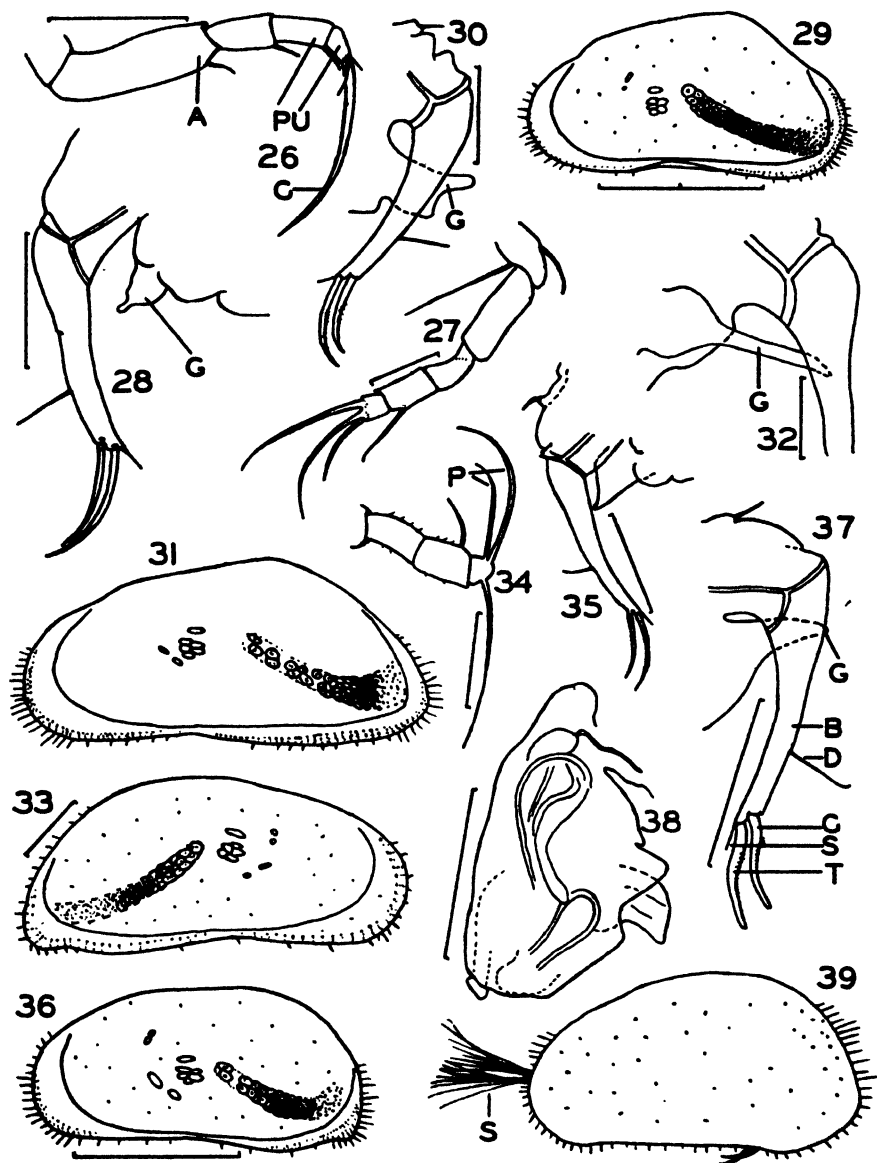


PLATE III

## PLATE IV

*Candona indigena* sp. nov.

FIG. 40.—View from outside of right valve of female (paratype). Scale as in fig. 41.

A—Anterior margin of shell	O—Ovary
C—Pore-canals	P—Posterior margin of shell
D—Dorsal margin of shell	S—Ventral sinuation
M—Muscle scars	V—Ventral margin

FIG. 41.—View from outside of left valve of male (paratype). Scale: 0.5 mm. T—Testis.

FIG. 42.—Dorsal view of female (holotype in alcohol). Scale as in fig. 41. S—Swimming setae of antennules.

FIG. 43.—Mandible (holotype). Scale: 0.1 mm. C—Chewing edge. P—Penultimate podomere. R—Branchial or respiratory plate. S—Setae bundle.

FIG. 44.—Distal podomeres of the second thoracic leg of male (allotype). Scale: 0.1 mm.

FIG. 45.—Third thoracic leg of female (holotype). Scale: 0.1 mm.

FIG. 46.—Furca and female genital lobe (paratype) with furcal ramus extended posteriorly. Scale as in fig. 45. G—Genital lobe.

FIG. 47.—Prehensile palps (allotype); (a) right palp seen from the inside; (b) left palp viewed from the outside. Scale as in fig. 45.

FIG. 48.—Penis (allotype). Scale: 0.1 mm. V—Vas deferens. O—Bifurcated outer lobe.

*Candona suburbana* sp. nov.

FIG. 49.—Inside view of right valve of female (allotype). Scale: 0.5 mm.

FIG. 50.—Inside view of right valve of male (paratype). Scale as in fig. 49.

FIG. 51.—Dorsal view of male (holotype; in alcohol). Arrow indicates the anterior end. Scale as in fig. 49.

FIG. 52.—Second thoracic leg of female (allotype). Scale: 0.1 mm.

FIG. 53.—Third thoracic leg of male (holotype). Scale as in fig. 52. S—Setae of the similarly directed pair. P—Divided penultimate podomere.

FIG. 54.—Proximal portion of the furcal ramus and the genital lobe of the female (allotype). Scale as in fig. 52. G—Genital lobe.

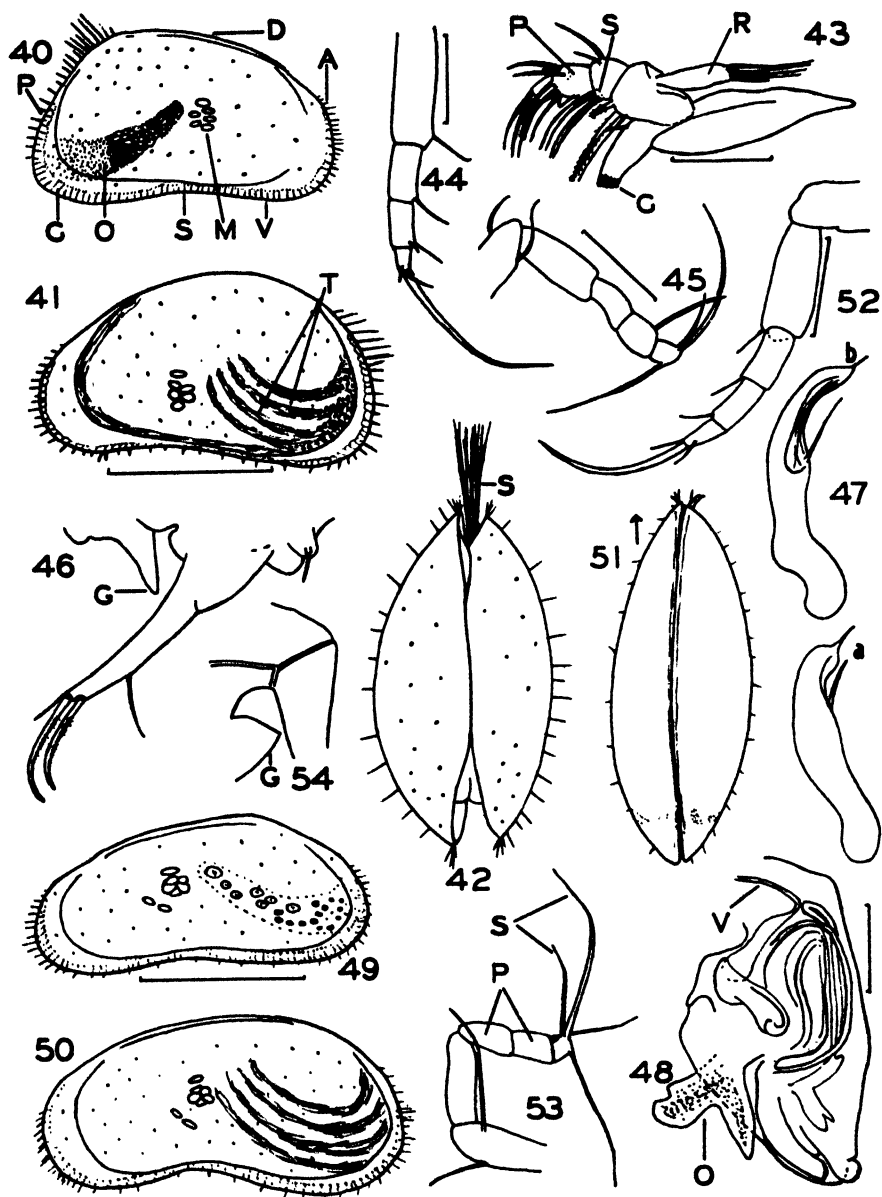


PLATE IV

## PLATE V

*Candona subarbana* sp. nov.

FIG. 55.—Furca of male (paratype). Scale: 0.1 mm.

FIG. 56.—Prehensile palps of male (paratype); (a) inside view of the left palp; (b) inside view of the right palp. Scale as in fig. 57.

FIG. 57.—Penis (paratype). Scale: 0.1 mm. I—Inner lobe of penis. M—Middle lobe of penis. O—Outer lobe of penis. V—Vas deferens.

*Candona fossulensis* sp. nov.

FIG. 58.—Inside view of left valve of female (holotype). Scale: 0.5 mm.

FIG. 59.—Markings on posterior slope of shell of female (paratype). Scale as in fig. 55.

FIG. 60.—Mandibular palp of female (paratype). Scale: 0.1 mm. S—Bundle of setae of antepenultimate podomere.

FIG. 61.—Third leg of female (paratype). Scale as in fig. 57.

FIG. 62.—Furca and genital lobe of female (paratype). Scale as in fig. 55.

FIG. 63.—Prehensile palps of male (allotype); (a) outside view of right; (b) outside view of left. Scale as in fig. 57.

FIG. 64.—Penis of male (paratype). Scale: 0.2 mm.

*Candona acuta* sp. nov.

FIG. 65.—Inside view of right valve of female (holotype). Scale: 0.5 mm.

FIG. 66.—View from ventrad of the left valve of female (holotype in alcohol). Arrow indicates anterior end. Scale as in fig. 65.

FIG. 67.—Second leg of female (paratype). Scale: 0.1 mm. F—First podomere. P—Penultimate podomere. S—Second podomere.

FIG. 68.—Third leg of female (paratype). Scale: 0.1 mm. P—Parts of the divided penultimate podomere.

FIG. 69.—Furca of the female (holotype). Scale: 0.1 mm.

B—Seta of dorsal-posterior  
part of the thorax

D—Dorsal seta of furca

G—Genital lobe

R—Ramus of furca

S—Terminal seta

T—Terminal claw

U—Subterminal claw

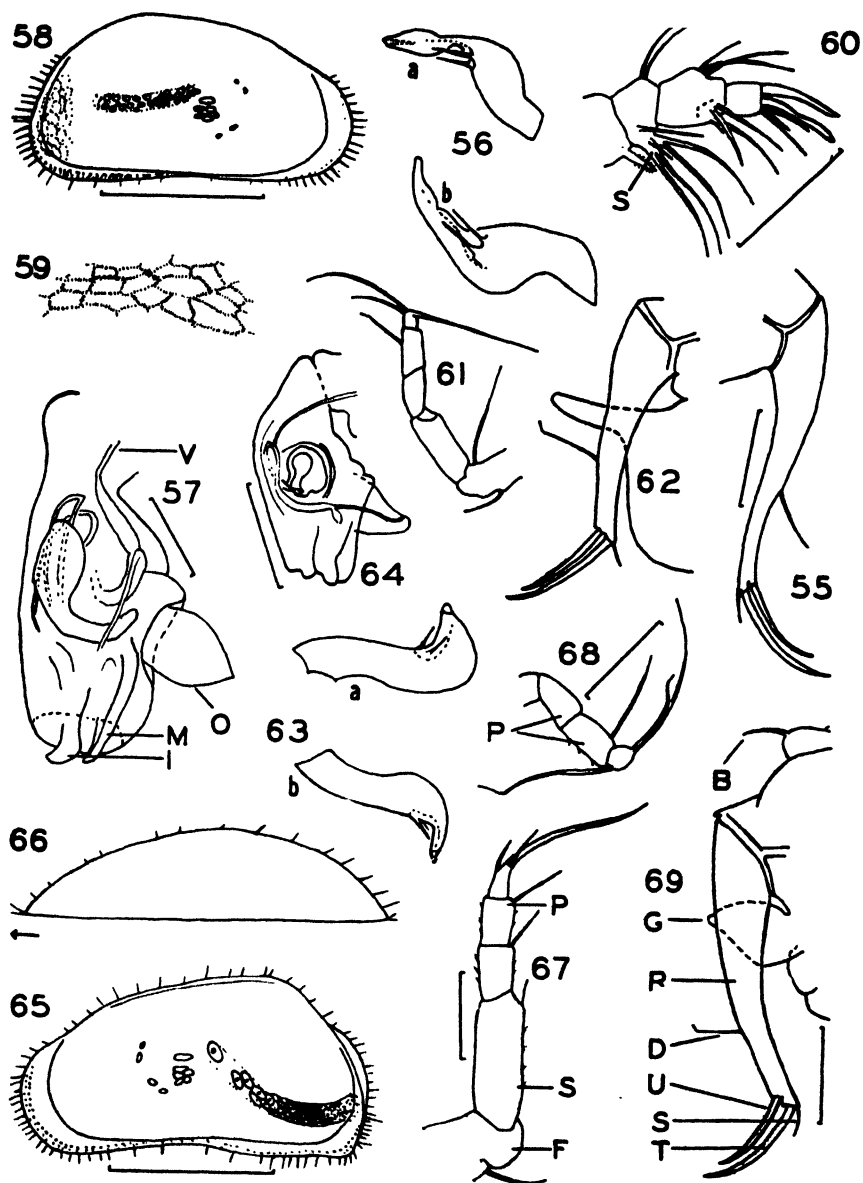


PLATE V

## PLATE VI

*Candona acuta* sp. nov.

FIG. 70.—Inside view of left valve of male (allotype). Scale: 0.5 mm.

FIG. 71.—Prehensile palps of the male (paratype); (a) inside view of left palp; (b) inside view of right palp. Scale: 0.1 mm.

FIG. 72.—Penis (allotype). Scale: 0.2 mm. I—Inner lobe. M—Middle lobe. O—Outer lobe.

*Cyclocypris forbesi* Sharpe 1897; female.

FIG. 73.—Inside view of left valve of shell. Scale: 0.25 mm.

FIG. 74.—Second thoracic leg. Scale: 0.1 mm.

FIG. 75.—Third thoracic leg. Scale as in fig. 74.

*Cypria turneri* sp. nov.

FIG. 76.—View of the left side of the female (paratype in alcohol). Scale: 0.25 mm. A—Swimming setae of antennae. E—Eye. M—Muscle scars. S—Swimming setae of antennules.

FIG. 77.—Ventral view of the left valve of female (in alcohol). The arrow points toward the anterior end.

FIG. 78.—Characteristic markings on the shell. Scale: 0.025 mm.

FIG. 79.—Furca of male (paratype). Scale: 0.1 mm.

FIG. 80.—Prehensile palps of the male (allotype); (a) left palp seen from inside; (b) right palp viewed from outside. Scale as in fig. 79. D—Dactylus. P—Propodus.

FIG. 81.—Penis of male (paratype). Scale as in fig. 79. I—Inner lobe. M—Middle lobe.

*Cypria mediana* sp. nov.

FIG. 82.—Outside view of right valve of female (paratype). Scale: 0.5 mm.

FIG. 83.—Ventral view of left valve of female (holotype in alcohol). Arrow indicates the anterior end. Scale as in fig. 82.

FIG. 84.—Third thoracic leg of female (holotype). Scale: 0.1 mm.

FIG. 85.—Furca of female (paratype). Scale as in fig. 84.

FIG. 86.—Inside view of right valve of male (allotype). Scale as in fig. 82.

FIG. 87.—Penis (allotype). Scale as in fig. 84.

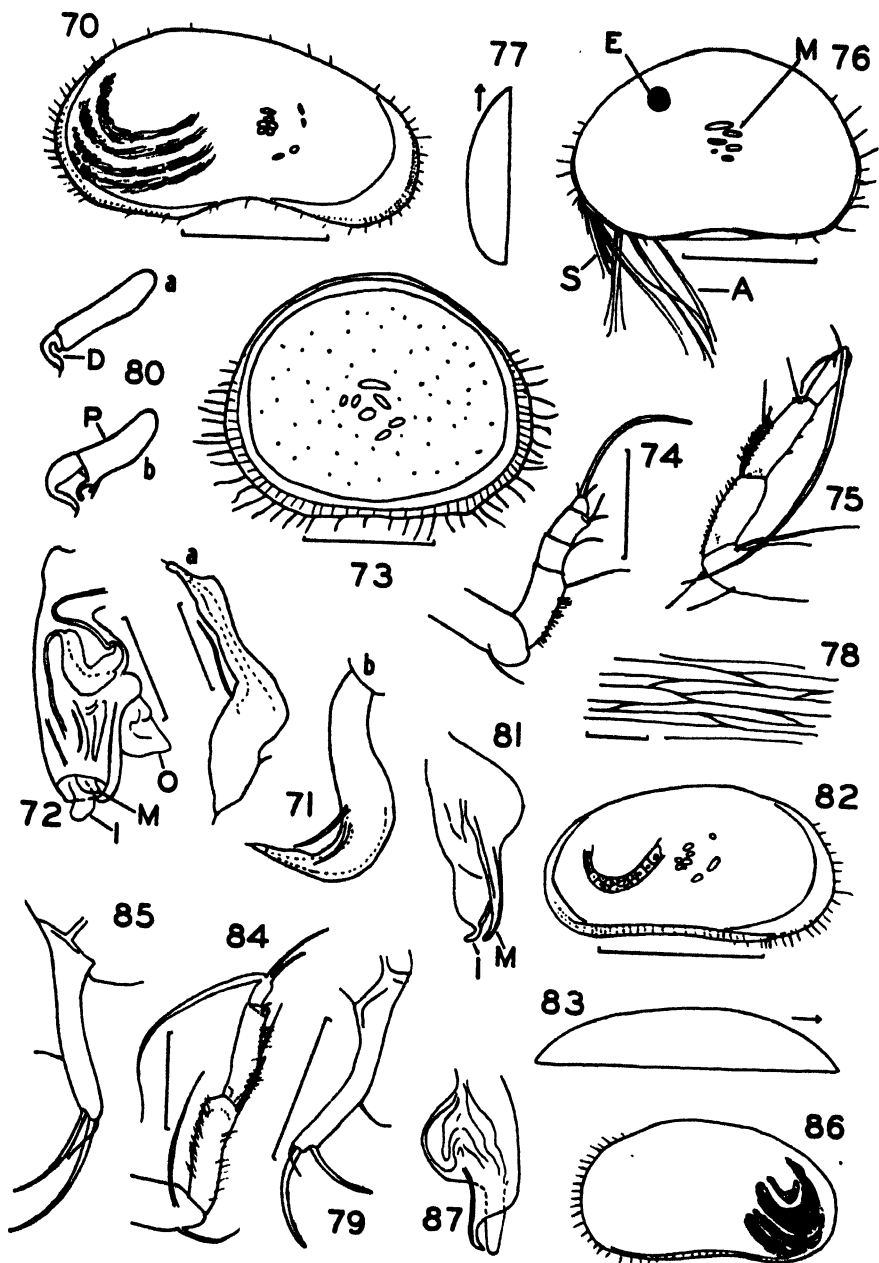


PLATE VI

## PLATE VII

*Cypria obesa* Sharpe 1897; female.

FIG. 88.—Inside view of right valve. Scale: 0.5 mm.

FIG. 89.—Distal portion of the third thoracic leg. Scale: 0.1 mm.

*Cypria maculata* sp. nov.

FIG. 90.—Inside view of left valve of female (holotype). Scale: 0.25 mm.

FIG. 91.—Third thoracic leg of female (paratype). Scale as in fig. 89.

FIG. 92.—Furca of female (holotype). Scale as in fig. 89.

FIG. 93.—Ductus ejaculatorius of the male. Scale as in fig. 89.

FIG. 94.—Prehensile palps of male: (a) outside view of left palp; (b) inside view of right palp. Scale: 0.05 mm.

FIG. 95.—Penis. Scale as in fig. 94. I—Inner lobe. M—Middle lobe.

*Cypria ophthalmica* (Jurine 1820) Brady and Norman 1889; female.

FIG. 96.—Animal viewed from left side. Scale: 0.25 mm.

FIG. 97.—Pattern of color markings on the shell. Scale: 0.05 mm.

*Physocypria pustulosa* Sharpe 1897; female.

FIG. 98.—Right valve viewed from the inside. Scale as in fig. 96.

*Ilyocypris gibba* (Ramdohr 1808) Brady and Norman 1889; female.

FIG. 99.—Right valve seen from the outside. (Sculpturing shown only on the posterior part of the shell.) Scale: 0.5 mm. F—Furrows. M—Flat-tened margin. P—Protuberances.

FIG. 100.—Second thoracic leg. Scale: 0.1 mm.

*Ilyocypris bradyi* Sars 1890; female.

FIG. 101.—Left valve seen from outside. (Shell sculpturing shown only on posterior part of shell.) Scale as in fig. 99.

FIG. 102.—Distal portion of the second thoracic leg (mounted in glycerine). Scale as in fig. 100. P—Two divisions of the penultimate podomere.

*Cypricercus tuberculatus* (Sharpe 1908) comb. nov.

FIG. 103.—Outside view of right valve of female. Arrow indicates anterior end. Scale: 0.5 mm.

FIG. 104.—Penis. Scale: 0.1 mm.

*Cypricercus reticulatus* (Zaddach 1844) Sars 1928.

FIG. 105.—Outside view of the right valve of female. Scale: 0.5 mm.

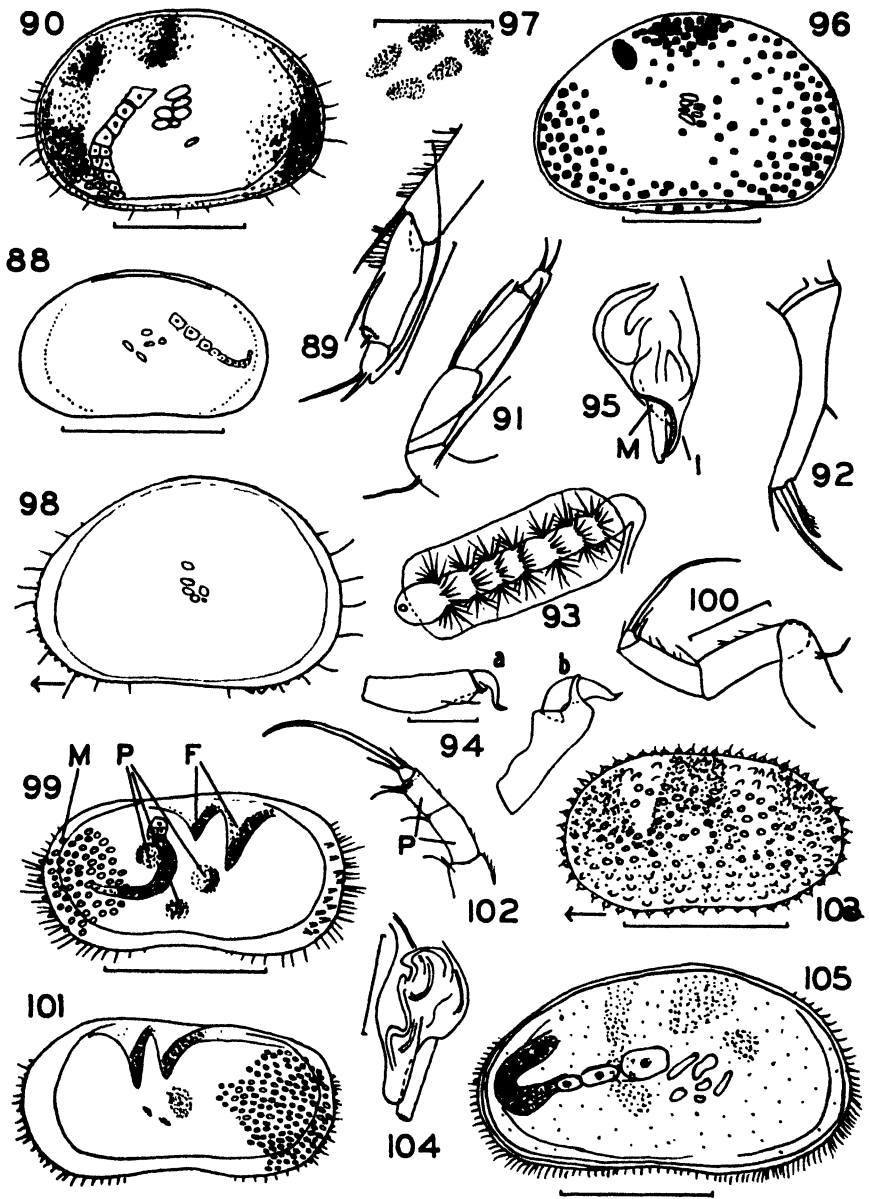


PLATE VII

## PLATE VIII

*Cypricercus reticulatus* (Zaddach 1844) Sars 1928.

FIG. 106.—Portion of the antenna of the female. Scale: 0.1 mm. A—Antepenultimate podomere. B—Seta with bulbous base. O—Sensory organ. S—Swimming setae.

FIG. 107.—Furca of female. Scale: 1.5 mm.

FIG. 108.—Outline drawing of the shell of the male. Arrow indicates the anterior end. A—Anterior portion of testis. P—Posterior portion of testis.

FIG. 109.—Penis. Scale as in fig. 106. L—Middle lobe. V—Vas deferens.

*Cyprinotus incongruens* (Ramdohr 1808) Turner 1895; female.

FIG. 110.—Inside view of right valve. Scale: 1.0 mm.

FIG. 111.—Furca. Scale: 0.5 mm.

*Notodromas monacha* (O. F. Müller 1776) Lilljeborg 1853; male.

FIG. 112.—Outside view of the left valve. Arrow indicates the anterior end. Scale: 0.5 mm.

FIG. 113.—Outer masticatory process of the maxilla. Scale: 0.05 mm.

FIG. 114.—Furca. Scale: 0.25 mm.

*Cypridopsis vidua* (O. F. Müller 1776) Brady 1867; female.

FIG. 115.—View of left side. Arrow indicates the anterior end. Scale: 0.5 mm.

FIG. 116.—Anterior margin of the right valve to show the tubercles. Scale: 0.1 mm.

FIG. 117.—Furca. Scale: 0.1 mm. F—"Flagellum."

*Potamocypria smaragdina* (Vávra 1891) Daday 1900.

FIG. 118.—Female viewed from the right side. Scale: 0.25 mm. C—Claws of second thoracic legs. S—Swimming setae of antennae.

FIG. 119.—End of maxillary palp to show distally widened ultimate podomere. Scale: 0.025 mm.

FIG. 120.—Outside view of terminal end of the right third thoracic leg to show the chela or "pincers apparatus."

FIG. 121.—Outside view of left valve of the male. Arrow points to the anterior end. Scale: 0.25 mm. A—Anterior portion of the testis. F—Anterior flange of shell.

FIG. 122.—Prehensile palps of the male; (a) outside view of the left palp; (b) inside view of the right palp. Scale: 0.05 mm. D—Dactylus. P—Propodus.

FIG. 123.—Ductus ejaculatorius of male. Scale as in fig. 122. V—Vas deferens.

FIG. 124.—Penis. Scale: 0.1 mm.

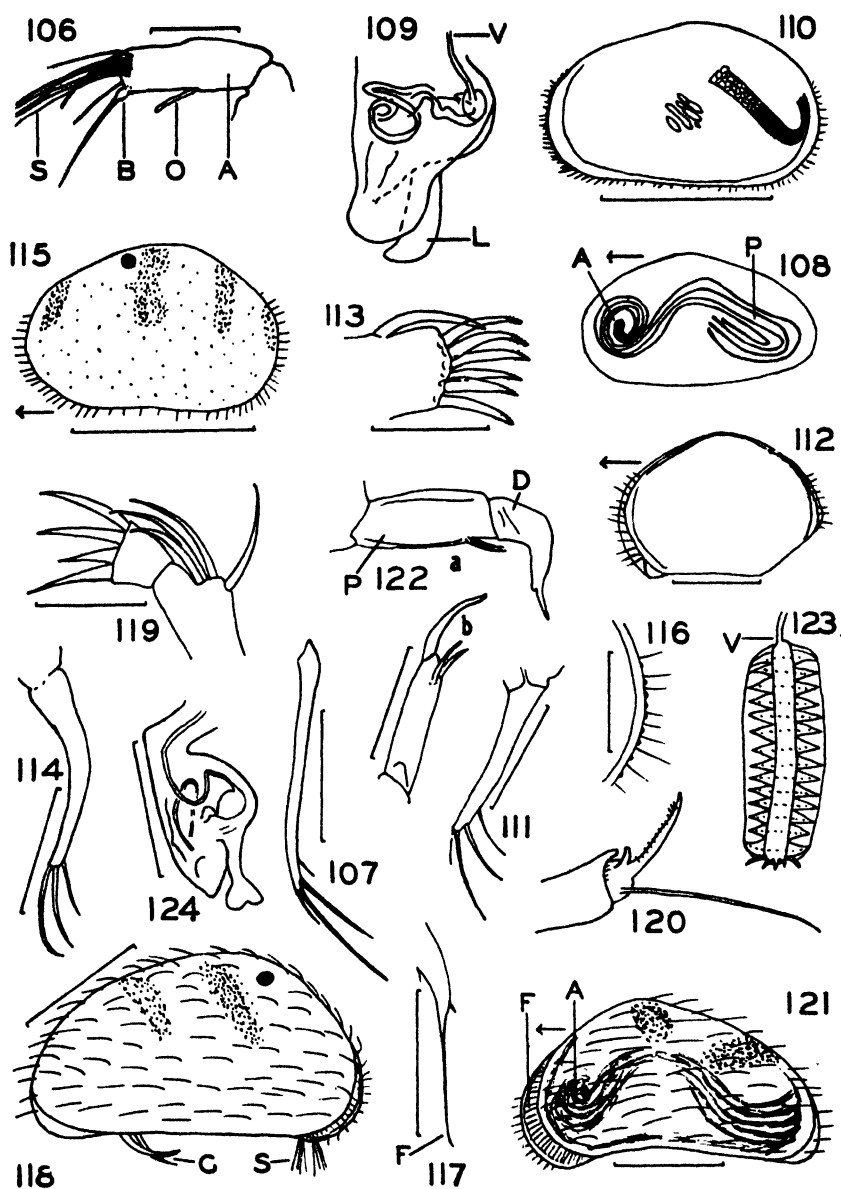


PLATE VIII

## PLATE IX

*Darwinula stevensoni* (Brady and Robertson 1870) Brady and Norman 1889; female.

FIG. 125.—Inside of left valve. Scale: 0.25 mm.

FIG. 126.—End of thorax. Arrow points ventrally. Scale: 0.05 mm.

*Limnocythere verrucosa* sp. nov.

FIG. 127.—Outside view of right valve of female. (Sculpturing omitted.) Scale as in fig. 125. F—Furrows. M—Anterior margin with pore-canals. P—Protuberances. S—Muscle scars.

FIG. 128.—A portion of the anterior margin of the shell. Scale: 0.1 mm. H—Setae. P—Pore-canals. S—Sculpturing. T—Tubercles.

FIG. 129.—Shell of female from above. Arrow indicates the anterior end. Scale as in fig. 125.

FIG. 130.—End of the antennule of the female to show the terminal and subterminal setae. Scale as in fig. 126. F—Fused portion of terminal setae.

FIG. 131.—View from the outside of the left antenna of the female. Scale: 0.1 mm. A—Articulation of parts of "flagellum." F—Basal portion of "flagellum" or exopodite. T—Antepenultimate podomere or first podomere of the endopodite.

FIG. 132.—Furca of female. Scale: 0.025 mm. P—Papilla with dorsal seta.

FIG. 133.—Outside view of right valve of male. (Surface markings not shown.) Scale as in fig. 125.

FIG. 134.—Outside view of right penis. Scale: 0.1 mm. F—Furca.

FIG. 135.—"Brush-form" sensory organ of male. Scale: 0.05 mm. B—Pedicel to which organ is attached. S—Distal setae.

*Limnocythere reticulata* Sharpe 1897.

FIG. 136.—Inside view of the left valve of the female. Scale: 0.5 mm.

FIG. 137.—Anterior and posterior ends of inside of the dorsal margin of the right valve of female to show the teeth. (Center of dorsal margin omitted.) AT—Anterior teeth. PT—Posterior teeth.

FIG. 138.—Furca of female. Scale: 0.05 mm. D—Dorsal seta.

FIG. 139.—Third thoracic leg of the male. Scale: 0.1 mm.

FIG. 140.—Shell of male viewed from the right side. Scale as in fig. 136.

FIG. 141.—Penis in outside view from the left. Scale: 0.25 mm.

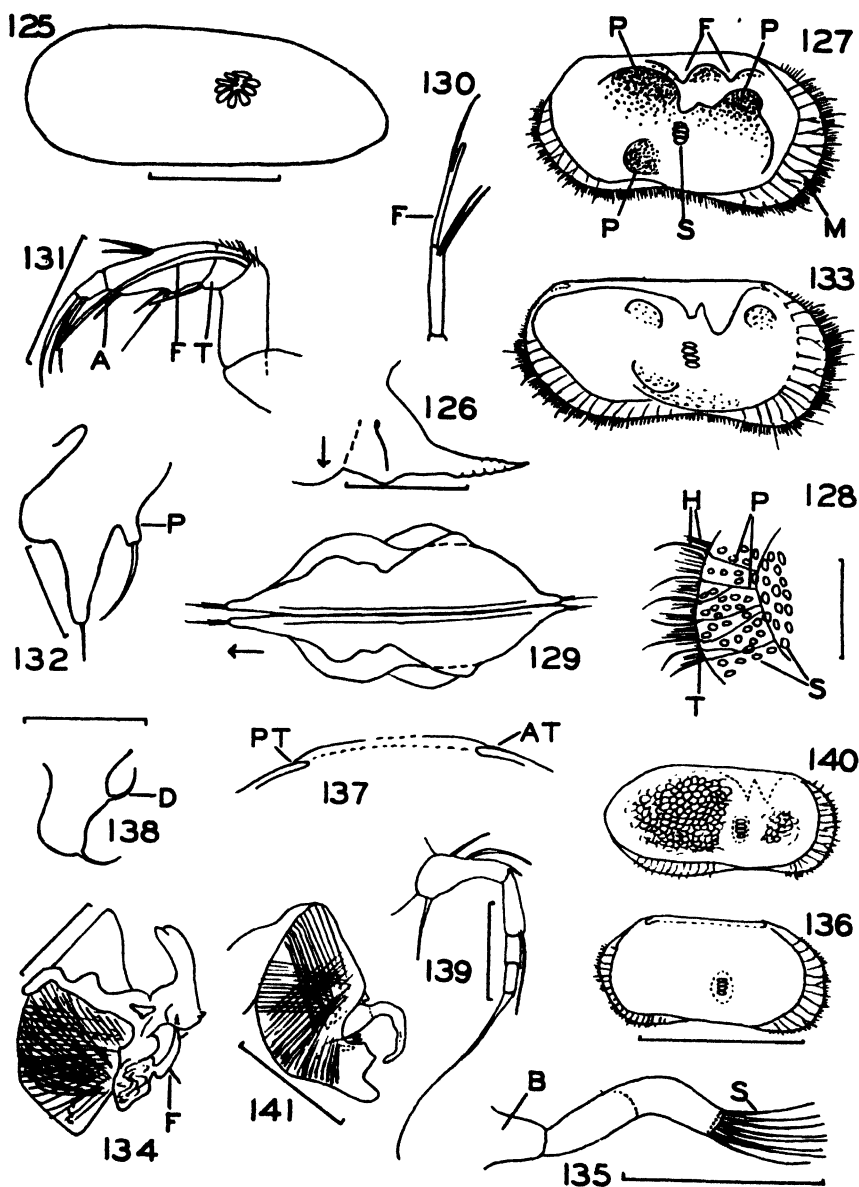


PLATE IX

## INDEX

The names of new species are printed in **bold-face** type. The names of other species known from Illinois and the page numbers referring to specific diagnoses are given in *italics*.

- Abdomen, 42, 46
- Acanthocephala, parasitic on ostracods, 10
- acuminata, Candona, 70; 73
- Acuminata, group of genus Candona, 55, 73-75
- acuta**, Candona, 16, 23, 25, 27, 28, 30, 34, 37, 40, 56, 57, 75, 82, 95, 96-100
- aemonae, Candona, 73
- affinis, Cypris, 139, 141
- albicans*, Candona, 16, 23, 25, 27, 30, 33, 34, 37, 40, 66, 67-69, 72
- Antenna, 43
- Antennules, 43
- Appendages, 42-46
- Associations between ostracod species, 32
- aurea, Argilloecia, 157
- aurea, Darwinula, 158
- Bairdia, genus, 51
- Bairdiidae, family, 51
- biangulata**, Candona, 16, 23, 25, 27, 30, 33, 34, 36, 40, 66, 67, 70-73
- bilobata, Candona, 72
- Biotic relationships, 29-33
- Body segmentation, 42
- bradii, Ilyocypris, 130
- bradyi*, Ilyocypris, 16, 23, 25, 27, 28, 30, 34, 37, 40, 127, 128, 130-131
- "Brush-form" organ, 46
- burlingtonensis, Cyprinotus, 135, 136, 137
- burlingtonensis, Cypris, 135, 136, 137, 138
- Candida, group of genus Candona, 55
- Candocypris, genus, 101
- Candocyprinae, subfamily, 52, 101
- Candona, genus, 54-57
- Candoninae, subfamily, 52-53
- Candoninae *s. str.*, subfamily, 52, 53-54, 101
- caudata*, Candona, 16, 23, 25, 27, 34, 36, 40, 56, 57, 74, 80-82, 92, 98
- Cephalic appendages, 42-45
- Chela of third leg, 46
- cingalensis, Cyprinotus, 136
- Circulatory system, 47
- Cladocopa, suborder, 50
- Cleaning foot, 46
- Color of shell, 32-33
- Compressa, group of genus Candona, 55, 56, 66-67
- compressa, variety of Potamocypris smaragdina, 154, 156
- copiosa*, Entocythere, 16, 166
- Copulatory organs, 48-49
- crogmani, Candona, 79-80
- crogmaniana*, Candona, 16, 23, 24, 27, 34, 37, 40, 56, 74, 79-80
- Cryptocandona, group of genus Candona, 55
- Cyclocyprinae, subfamily, 52-53, 100-101
- Cyclocypris, genus, 101-102
- Cypria, genus, 101, 104-105
- Cypricercus, genus, 132-133
- Cypridae, family, 51-53
- Cypridopsinae, subfamily, 52-53, 132, 150
- Cypridopsis, genus, 150-151
- Cyprinae *sensu lato*, subfamily, 52, 132
- Cyprinae *s. str.*, subfamily, 52-53, 131-132
- Cyprinotus, genus, 132, 143
- Cyprois, genus, 147, 149
- Cytherella, genus, 51
- Cytherellidae, family, 50
- Cytheridae, family, 51, 159
- Darwinula, genus, 157
- Darwinulidae, family, 51, 157
- decora, Candona, 91, 95
- dentifera, Cypria, 125, 127
- dentifera*, Physocypris, 16, 37, 40, 116-117, 120-121, 125-127
- Digestive system, 47
- distincta*, Candona, 16, 23, 24, 27, 33, 34, 37, 40, 56, 57, 74, 77-78, 91
- Distribution, 25-29, 39-41
- Ductus ejaculatorius, 48
- Egg-laying, 37-38
- elegantula, Cypria, 106, 107, 108-109
- elongata, Candona, 80, 88, 91-92
- Entocythere, genus, 166
- Entocytherinae, subfamily, 159, 166
- eriensis, Candona, 91
- Eucypris, genus, 133
- Excretory system, 47
- exculpta, Cypria, 38, 106, 109
- exilis, Candona, 62, 65, 66
- Exopodite of antenna, 43, 51
- exsculpta, Cypria, 22, 29, 106, 108-110
- Eyes, 43

- fabaeformis*, Candona, 76-77, 100  
*Fabaeformis*, group of genus Candona, 55, 100  
*fasciata*, Cypris, 35  
*fasciata*, Dolerocypris, 35  
Feeding, appendages, 44-45  
*fluviatilis*, Candona, 16, 23, 24, 27, 28, 33, 34, 36, 40, 56, 57, 58, 60-62  
Food of ostracods, 38-39  
*forbesi*, *Cyclocypris*, 16, 23, 24, 27, 31, 32, 34, 37, 40, 102-103  
*fossulensis*, Candona, 16, 23, 24, 27, 33, 34, 37, 40, 56, 57, 75, 92-95, 98  
Furca, 46  
Furcal ramus, 43, 46  
*fuscata*, Cypris, 135, 136, 137, 138, 139, 142  
*fuscatus*, *Cypricercus*, 17, 36, 40, 133, 135-138  
*fuscatus*, Monoculus, 135  
*gibba*, Cypris, 128  
*gibba*, *Ilyocypris*, 16, 23, 25, 27, 28, 30, 34, 37, 40, 127, 128-130, 131  
*gigantica*, variety of *Eucypris fuscata*, 135, 137  
*globula*, *Physocypris*, 10, 121-125  
Habitats, 21-29  
Heart, 47  
Herpetocypridinae, subfamily, 52  
*herricki*, Cypris, 35, 36  
*hertzogi*, Candona, 72  
*hirsuta*, *Eucypris affinis*, 139, 140, 141, 142, 143  
*hirsutus*, *Cypricercus affinis*, 142  
*horridus*, *Cypricercus*, 135  
Hydrogen ion concentration, 28-29  
*Iliocyrella*, genus, 127-128  
*illinoisensis*, *Entocythere*, 16, 166  
*illinoisensis*, *Limnocythere*, 165  
*illinoisensis*, *Limnocythere*, 17, 37, 40, 161, 162, 165-166  
*Ilyocyprinae*, subfamily, 52-53, 127-128  
*Ilyocypris*, genus, 127-128  
*improvisa*, *Darwinula*, 158  
*incisa*, *Chlamydotheca*, 36  
*incongruens*, *Cyprinotus*, 17, 23, 25, 26, 27, 28, 30, 34, 35, 37, 38, 40, 46, 143, 144-145, 146-147  
*incongruens*, Cypris, 144  
*indigena*, Candona, 16, 23, 24, 27, 33, 34, 37, 40, 56, 57, 75, 85-88, 98  
*labiata*, *Chlamydotheca*, 36  
*labiata*, Cypris, 36  
*laevis*, *Cyclocypris*, 103-104  
*lapponica*, Candona, 87-88  
Larval development, 35-38  
*levanderi*, Candona, 87-88  
*Limnocythere*, genus, 160  
*Limnocythere*, genus, 160-161  
*Limnocytherinae*, subfamily, 159-160  
*Macrocyprinae*, subfamily, 52  
*maculata*, *Cypria*, 16, 23, 25, 27, 29, 30, 33, 34, 37, 40, 105, 114-117, 119, 126-127  
major, variety of *Cypris fuscata*, 135, 137  
Mandibles, 44  
*marginata*, Cypris, 149  
*marginata*, *Cyprois*, 15, 17, 37, 40, 41, 149-150  
Masticatory processes, 44, 45  
Maxilla, 44  
Maxillary foot, 45  
Maxilliped, 45  
*mediana*, *Cypria*, 16, 23, 25, 27, 28, 34, 37, 40, 41, 105, 110-112  
Methods of collection and study, 17-21  
minor, variety of *Cypris fuscata*, 137, 139-140  
*Mixta*, group of genus Candona, 55  
*monacha*, Cypris, 148  
*monacha*, *Notodromas*, 15, 17, 23, 24, 27, 34, 37, 38, 40, 41, 148-149  
*monachus*, *Notodromas*, 148  
*Myodocopa sensu lato*, order, 50  
*Myodocopa s. str.*, order, 50  
Nauplius, 35  
*neglecta*, *Cypria*, 119  
Nervous system, 47-48  
*Nesidea*, genus, 51  
*Nesideidae*, family, 51  
*Notodromas*, genus, 147, 148  
*Notodrominae*, subfamily, 52-53, 132, 147  
*obesa*, *Cypria*, 16, 23, 25, 27, 30, 33, 34, 37, 40, 105, 112-114  
*obesa*, *Cypridopsis vidua*, 151, 152  
Ontogeny, 35-36  
*ophthalmica*, *Cypria*, 16, 23, 24, 27, 28, 29, 30, 31, 33, 34, 37, 40, 105, 108, 114, 116-117, 117-120  
*ophthalmicus*, Monoculus, 117  
*ophthalmica*, *Cypria*, 114, 117  
Ostracoda, order, 49  
Ostracoda, suborders of, 49-50  
Ovary, 48  
ovum, *Cyclocypris*, 35  
ovum, Cypris, 35  
Palps, 44, 45  
*Paracandona*, genus, 54  
*parallela*, Candona, 66, 67-69

- Parasites of ostracods, 10  
 pellucida, Cypris, 146  
 pellucida, Cyprinotus, 144, 146-147  
 pellucidus, Cyprinotus, 17, 36, 40, 143, 145, 146-147  
 Penis, 48-49  
 Physocyprina, genus, 101, 120-121  
 Plankton, 29-30  
 Plants, relation of ostracods to, 30-32  
 Platycopa, suborder, 50  
 Podocopa *sensu lato*, suborder, 50-51  
 Podocopa *s. str.*, suborder, 49-51  
 Pontocyprinae, subfamily, 52  
 Potamocypris, genus, 150, 153  
*punctata*, Candona, 16, 23, 24, 27, 33, 34, 37, 40, 41, 56, 57, 58-60  
*pustulosa*, Cypria, 29, 121  
*pustulosa*, Cypridopsis, 151-153  
*pustulosa*, Physocyprina, 10, 11, 16, 23, 24, 27, 28, 29, 30, 32, 33, 34, 37, 40, 120, 121-125  
*retlicauda*, Candona, 16, 37, 40, 56, 57, 74, 75-76  
*reflexa*, Candona, 62, 65  
 Reproduction, 36-38  
 Reproductive system, 48-49  
 Respiration, 46  
*reticulata*, Cypris, 139  
*reticulata*, Limnocythere, 163  
*reticulata*, Limnocythere, 17, 23, 25, 27, 28, 29, 30, 32, 34, 37, 40, 161, 163-165  
*reticulatus*, Cypricercus, 17, 23, 24, 26, 27, 30, 33, 34, 36, 37, 38, 40, 133, 137, 138, 139-143  
 Rostrata, group of genus Candona, 55, 57-58  
*scopulosa*, Candona, 91  
 Seasonal distribution, 33-34  
 Sensory organs, 43, 48  
*sharpei*, Candona, 16, 37, 40, 56, 74, 76-77, 100  
*sharpei*, Cyclocypris, 16, 37, 40, 103-104  
 Shell, morphology, 41-42  
*sigmoides*, Candona, 16, 23, 24, 27, 28, 34, 37, 40, 56, 74, 82-84, 98  
*simpsoni*, Candona, 16, 23, 25, 27, 29, 30, 33, 34, 36, 40, 56, 57, 58, 62-66  
*smaragdina*, Cypridopsis, 154  
*smaragdina*, Potamocypris, 17, 23, 25, 26, 27, 28, 29, 30, 31, 32, 33, 34, 37, 38, 39, 40, 153, 154-157  
*speciosa*, Chlamydotheca, 35  
 Spirocypris, genus, 134-135  
*stagnalis*, Candona, 68  
*stevensoni*, Darwinula, 15, 17, 23, 24, 27, 34, 37, 40, 41, 157-159  
*stevensoni*, Polychaetes, 158  
*striolata*, Cypria, 106  
*suburbana*, Candona, 16, 23, 24, 27, 33, 34, 37, 40, 56, 57, 75, 88-92, 98  
 Tactile sense organs, 48  
 Testes, 48  
*testudinaria*, Cypris, 139, 140-141  
 Thoracic appendages, 45-46  
*tuberculata*, Spirocypris, 133-135  
*tuberculatus*, Cypricercus, 16, 23, 24, 27, 33, 34, 37, 40, 41, 133-135  
*turneri*, Cypria, 16, 22, 23, 25, 27, 29, 30, 33, 34, 37, 38, 40, 105, 106-110  
*verrucosa*, Limnocythere, 17, 23, 24, 27, 31, 34, 37, 40, 41, 160, 161-163  
*vidua*, Cypridopsis, 11, 17, 23, 25, 27, 28, 29, 30, 31, 32, 33, 34, 36, 38, 39, 40, 151-153  
*vidua*, Cypris, 151  
 Zenker's organ, 48

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THE GENUS CONOTRACHELUS' DEJEAN  
(COLEOPTERA, CURCULIONIDAE)  
IN THE NORTH CENTRAL  
UNITED STATES

WITH NINE PLATES

BY  
HERBERT FREDERICK SCHOOF

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## PREFACE

The greater portion of the material included in this study has been taken from a thesis of the same title, submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Entomology in the Graduate School of the University of Illinois, 1940. The original material has been revised, and several additions have been made.

The author wishes to express his sincerest thanks to Professor W. P. Hayes, of the Department of Entomology, University of Illinois, under whose supervision this study was conducted. Professor Hayes suggested the problem and throughout the study has furthered its progress by his many helpful criticisms. He has given unstintingly of his time, and has also placed at the writer's disposal his excellent personal collection of *Conotrachelus*. It is with pleasure that the author names a new species, *C. hayesi*, in his honor.

Much credit is due Mr. L. L. Buchanan, of the United States National Museum, who has given generously of his time to discuss with the writer the problems involved in the genus, and who has been of much assistance during the entire course of the study. Mr. Buchanan has informed the writer of several morphological characters of taxonomic value in the genus, has arranged for specimen loans from the National Museum, and has assisted the writer in innumerable ways. The writer takes pleasure in naming a new species, *C. buchanani*, in his honor.

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*Raleigh, North Carolina*

H. F. S.

# CONTENTS

I. INTRODUCTION . . . . .	9
II. REVIEW OF LITERATURE . . . . .	9
III. MATERIALS AND METHODS . . . . .	12
A. The Removal, Study, and Preservation of the Male Genitalia. . . . .	12
B. Measurements . . . . .	14
C. Studies of Collections and Types . . . . .	15
D. Organization of Distributional Data . . . . .	16
IV. THE MORPHOLOGICAL CHARACTERS OF TAXONOMIC IMPORTANCE . . . . .	16
A. The Body Regions and Their Appendages . . . . .	17
B. Color and Vestiture . . . . .	23
C. Characters for Sex Determination . . . . .	24
D. The Male Genitalia . . . . .	25
V. NOMENCLATURE . . . . .	37
VI. CLASSIFICATION . . . . .	39
Key to Groups . . . . .	40
A. Group I (with Key to Species) . . . . .	40
<i>C. juglandis</i> Lec. . . . .	44
<i>C. nenuphar</i> (Hbst.) . . . . .	48
<i>C. buchanani</i> n. sp. . . . .	51
<i>C. albicinctus</i> Lec. . . . .	54
<i>C. iowensis</i> n. sp. . . . .	57
<i>C. retentus</i> (Say) . . . . .	60
<i>C. affinis</i> Boh. . . . .	65
<i>C. hickoriae</i> n. sp. . . . .	69
<i>C. falli</i> Blatch. . . . .	72
<i>C. nivosus</i> Lec. . . . .	73
<i>C. seniculus</i> Lec. . . . .	76
<i>C. elegans</i> (Say) . . . . .	80
<i>C. hayesi</i> n. sp. . . . .	85
<i>C. aratus</i> (Germ.) . . . . .	88
<i>C. tibialis</i> n. sp. . . . .	91

# ILLINOIS BIOLOGICAL MONOGRAPHS

## VI. CLASSIFICATION (*continued*)

B. Group II (with Key to Species) . . . . .	94
<i>C. crataegi</i> Walsh . . . . .	96
<i>C. adspersus</i> Lec. . . . .	99
<i>C. naso</i> Lec. . . . .	101
<i>C. carinifer</i> Casey . . . . .	104
<i>C. posticatus</i> Boh. . . . .	106
<i>C. recessus</i> (Casey) . . . . .	109
<i>C. geminatus</i> Lec. . . . .	111
<i>C. cribricollis</i> (Say) . . . . .	114
C. Group III (with Key to Species) . . . . .	118
<i>C. tuberosus</i> Lec. . . . .	119
<i>C. anaglypticus</i> (Say) . . . . .	121
<i>C. leucophaeatus</i> Fahr. . . . .	126
D. Group IV (with Key to Species) . . . . .	129
<i>C. fissunguis</i> Lec. . . . .	131
<i>C. erinaceus</i> Lec. . . . .	134

VII. ADDENDUM: <i>Conotrachelus carolinensis</i> n. sp. . . . .	136
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VIII. SUMMARY . . . . .	141
-------------------------	-----

IX. GLOSSARY . . . . .	142
------------------------	-----

X. LITERATURE CITED . . . . .	144
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PLATES . . . . .	149
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## I. INTRODUCTION

The genus *Conotrachelus* Dejean embraces over 930 known species, all of which are confined to the Americas. The majority of these species occur in South and Central America, 54 species being known from the United States and Canada. In spite of the relatively large number of species in this region, little taxonomical or morphological work has been done on the genus other than that included in general considerations of the Rhynchophora. Biological data have been accumulated on many of the species, but, as will be pointed out later, the significance of some of these data is questionable because of specific confusion. Consequently, a taxonomic revision of the genus would seem to be of definite value.

The investigations reported here have a threefold purpose; first, to prepare workable keys to, and descriptions of, the species of *Conotrachelus* occurring in Illinois and the surrounding states of Wisconsin, Iowa, Missouri, Kentucky, and Indiana; second, to study the morphology of the male genitalia and determine their taxonomic significance; and third, to evaluate the morphological characters previously used in the classification of this genus, and, if possible, to indicate additional ones. The majority of the species found in this middlewestern area are present over the eastern half of the United States, and the classification herein will, in general, apply to this eastern area.

## II. REVIEW OF LITERATURE

The taxonomic literature on the genus *Conotrachelus* has been confined to considerations in comprehensive works on the Rhynchophora and to descriptions of new species.

Dejean (1835) erected the genus *Conotrachelus*, but merely listed the species included. Schönherr (1837) was the first to bring together in a descriptive manner the known species of *Conotrachelus*. Of the sixty-five species discussed in Schönherr's *Genera et Species Curculionidum*, twelve occurred in the United States, and the remainder were from South or Central America. A key was given by Schönherr in which the final designation was to groups of species instead of to one species. The genus and many of the species were described in detail, but the majority of the descriptions were by Boheman and Fahreus, Schönherr having discussed only the generic characteristics. Most of the species were accredited to prior workers, but subsequent study has shown that many of these were *nomina nuda*; consequently, many new species were erected unknowingly. In 1845 Schönherr published another work on this genus, including at that time 106 species, of which thirteen were from the United States.

Leconte (1876) was the first American author to discuss the genus *Conotrachelus*. He separated it into four divisions, Division I consisting of parts A and B. In the appendix of the same publication Leconte amended his Division I, subdividing part B into two sections. The characters used to erect these groups are similar, except for modifications, to those used by the writer (p. 40). Leconte discussed twenty-four species in the text of his work, eleven of which were new. In the appendix, he described one other new species and stated that *plagiatus* n. sp. (p. 233) was a synonym of *nivosus* n. sp. (p. 229). The majority of the remaining thirteen species were redescribed, but several of them, such as *anaglypticus* (Say) and *leucophaeatus* Fahr., were only briefly mentioned. Leconte did not give any biological data, his discussion being confined to taxonomy and nomenclature.

Champion (1904) published the most comprehensive work on this genus, but his study, with the exception of four species, *posticatus* Boh., *leucophaeatus* Fahr., *anaglypticus* (Say), and *serpentinus* (Klug), was mainly concerned with the Central American fauna. Champion discussed 188 species, the majority of which were new. The characters of previously described species were briefly mentioned and each new species was fully described. The descriptions and discussions of the species were in numerous instances supplemented by figures, many of which were colored. The type of key employed was similar to that of Schönherr, the final designation being to a group of species. Champion's key, however, was condensed in a unit instead of being scattered through the text as was the case with Schönherr's.

Blatchley and Leng (1916) considered those species of *Conotrachelus* east of the Mississippi, treating twenty-eight, one of which was new. These authors followed Leconte's subdivisions of the genus, except that they listed them as Groups I to VI. All the species were redescribed and biological and distributional data were given.

The most recent treatment of the genus is that by Mutchler and Weiss (1925).<sup>\*</sup> These workers brought together the available biological data on the sixteen species occurring in New Jersey and discussed briefly the genus and these species, including a descriptive key to the latter. This paper is of much value for its biological discussions.

The six previously mentioned treatments are the only comprehensive works pertaining to the entire genus. Other references, briefly discussed below, are limited to descriptions of new species or to one section of the genus.

<sup>\*</sup>Dr. T. D. A. Cockerell, in Science, Vol. 92, No. 2397, December 6, 1940, reviews a British Museum Publication by K. Fiedler, entitled, "Monograph of the South American Weevils of the Genus *Conotrachelus*," February, 1940, 365 pages. According to the reviewer, this monograph treats approximately 600 species, of which 416 are new. It is well illustrated and is published in German. The writer, as yet, has been unable to examine a copy of this monograph; consequently, it is not mentioned in the review of literature.

The earliest description of a species of *Conotrachelus* was that of *nenuphar* by Herbst (1797).<sup>\*</sup> Germar, another European worker, described *aratus* in 1824. Say (1831), the first American author accredited with species of *Conotrachelus*, described *retentus*, *cribricollis*, *anaglypticus*, and *elegans*. Walsh (1864), Leconte (1878), and Casey (1892, 1910) also described new species. Schaeffer (1904, 1906) published descriptions of five new species and included in the 1906 paper a key to all the known species of Leconte's Division 1-A. Recent describers of new North American species have been Fall (1907, 1913, 1917, 1929), Blatchley (1917), and Van Dyke (1930). Buchanan (1937) published the synonymy of *C. atokanus* Fall and *Loceptes recessus* Casey.

The genus *Conotrachelus* and its species have also been considered in numerous catalogues. Dejean (1835, 1837) in his catalogue listed seventy-one specific names, of which sixty-seven were *nomina nuda*. Henshaw (1885, 1895) listed twenty-eight species north of Mexico in 1885, and in his Third Supplement (1895) added six more. Leng (1920) listed forty-eight species north of Mexico, and in his Second Supplement (1933) increased the total to fifty-three. The most recent catalogue is that by Hustache (1936), in the *Coleopterorum Catalogus* of Junk and Schenkling, in which fifty-four North American species are listed. While Henshaw and Leng considered only the North American species and their synonymy, the *Coleopterorum Catalogus* deals with all species of *Conotrachelus* and includes references to biological data as well. Several names are shown to be preoccupied, and new ones are substituted. The Leng catalogue and supplements, however, are the most reliable sources for references to original descriptions and distributional data. In the *Coleopterorum Catalogus*, the distribution of certain American species known from only one locality is frequently given as "*Etats Unis*." Some Cuban species also are erroneously reported as occurring in the United States. This catalogue, however, is preferred for biological references.

Most of the species mentioned in this review of literature, excepting those treated by Leconte (1876) and Blatchley and Leng (1916), are indigenous to the Gulf Coast States and the southwestern area. Consequently, this treatment of the species in the midwestern area will be principally concerned with those species discussed by Leconte (1876) and Blatchley and Leng (1916). Further references to these two works will be found under the discussions of the individual species.

The morphological literature is discussed under the section on morphology, and the nomenclatural references are included in the section on nomenclature.

<sup>\*</sup>All species before 1835 were placed in allied genera, as the genus *Conotrachelus* was not erected until that date.

### III. MATERIALS AND METHODS

#### A. THE REMOVAL, STUDY, AND PRESERVATION OF THE MALE GENITALIA

The initial step in the dissection of the male genitalia is the removal of the abdomen, since with museum specimens it is very difficult, if not impossible, to dissect out the genitalia with the abdomen *in situ*. Before this is attempted, however, the specimen should be relaxed, as it is desirable that the specimen be fully pliable before being handled. For manipulation, the insect, when unpinned is best held between the thumb and forefinger. The fingers possess a certain amount of pliability which cannot be obtained with forceps; the latter frequently slip and cause the insect to be violently expelled. With the specimen in place, a sharply pointed, flattened needle is gradually inserted between the abdomen and the metacoxa. When the needle enters the coxal cavity it is slowly turned so that the flattened point acts as a lever forcing the abdomen to separate from the metacoxae and the metasternum. The needle is then moved medially to sever the connecting tissues and to further separate the abdomen from the metasternum. In some instances only one manipulation of the dissecting needle is necessary; in others several different insertions may be required. While removing the abdomen the specimen should be held firmly so that the elytra do not become disengaged; otherwise they may become permanently "sprung."

The removed abdomen is placed in a cold solution of concentrated potassium hydroxide, the period of immersion in this solution varying with the specimen, the larger ones requiring approximately one hour, the smaller ones thirty minutes. It is best to soak the abdomen in potassium hydroxide only until the muscles have softened, rather than until they have broken down completely, since the length of time necessary for muscular disintegration may lead to undesirable softening effects upon the genitalia.

After removal from the potassium hydroxide solution, the abdomen is washed in water and placed in a few drops of water upon a slide. With the dorsal surface of the abdomen upwards, a needle is placed basally within the body cavity to hold the structure in position. When secure, a lengthwise incision is made along each side of the dorsum at its line of junction with the pleural region. The latter is heavily sclerotized, while the first six terga are membranous. The seventh and eighth terga, however, are sclerotized and fit tightly against the pleura (see Fig. 10), so progress in cutting here is slow and difficult. Care must be taken at these points to keep the cutting instrument as near to the pleura as possible, since the male genitalia lie close to the lateral walls of the seventh and eighth terga. When the incisions have been completed, the dorsum, genitalia, and eighth sternum may be removed in mass from

their normal position. Muscles and intestine are then removed and the genitalia may be easily seen attached to the eighth segment. Since they are fastened to the body wall by a membrane (Fig. 8, 1st connecting membrane), this must be severed both dorsally and ventrally to release the genitalia. Once the membrane is cut the genitalia are free and can be removed to a storage vial.

The technique discussed above was the one usually employed, but in many cases digressions from it were necessarily made, depending on the condition of the specimen to be dissected. Sometimes it was not necessary to remove the dorsum completely, but merely to sever it half-way and then by pressure upon the genitalia to force them outward. Occasionally potassium hydroxide was not employed, especially with freshly-emerged specimens where the genitalia already were soft. Other variations in the method occurred repeatedly because of the differences in the age, size, and condition of the specimens.

After the genitalia have been removed, the dorsum is replaced on the sclerotized sterna and pleura of the abdomen. The entire abdomen is then allowed to dry, and the dorsum upon drying adheres firmly to the sterna and pleura. Following this, the abdomen with its ventral surface upwards is fastened by an adhesive to the card point bearing the specimen. In this position the punctation of the abdominal sterna is readily accessible for study. The abdomen may be replaced in the specimen, but this is difficult and damage to the specimen may result. Such replaced abdomens cannot be fastened as securely as they can be on card points and they may later drop off.

The genitalia were temporarily stored in vials in a solution of 70% ethyl alcohol or in a three-to-one mixture of 70% alcohol and glycerine. The former was preferred since it did not show the tendency to "creep" up the sides of the vials as did the mixture of alcohol and glycerine.

Genitalia to be studied comparatively were placed in glycerine-filled depression slides which had perpendicular wells. For drawing and detailed study of the genitalia a syracuse watch glass half-filled with paraffin was used. A layer of glycerine or alcohol was poured over the paraffin and the genitalia then fastened in position by means of a *minuten nadeln*. It was only by this method that the genitalia could be securely fastened in position. Cotton, sand, and glass chips were unsatisfactory for this purpose. Light reflected up through the paraffin provided a satisfactory background. Glycerine invariably worked down under the paraffin and loosened it, and new study dishes had to be prepared every month.

For permanent preservation of the genitalia the following method was employed: a cork disc  $\frac{1}{16}$ " thick and 10 mm. in diameter, with a hole 4 mm. in diameter slightly off center, was attached to the insect pin bearing the specimen. A 7 mm. circular coverslip was then fastened to the

ventral surface of the disc by means of Canada balsam. If desired the coverslip could be fastened to the disc before the latter was attached to the pin. A thin layer of balsam was next placed in the resultant cavity, and the genitalia arranged in this layer. Previous to this arrangement, the genitalia had been immersed in absolute alcohol from one to five minutes. The disc was then set aside for 24-48 hours until the balsam hardened. This firmly fixed the genitalia in position so that when the remainder of the balsam was added the genitalia did not float about. The surface tension of the thin layer kept the genitalia in position until the hardening occurred. Genitalia placed directly in a thick layer of balsam would rarely stay in position even though the disc was kept horizontal. At the end of the hardening period the entire cavity was filled with balsam and another coverslip fitted over the dorsal surface of the disc. The mount was then gently heated to drive off any air bubbles, after which it was stored in a horizontal position to prevent the genitalia from slipping to one side of the disc. If the mount was tilted excessively, the genitalia would shift their position even though the balsam had been preliminarily hardened. After the balsam hardened entirely it was possible to tilt the disc in any direction, at least temporarily, without the genitalia moving. Occasionally frass from the sides of the hole would get into the balsam, but this difficulty was overcome by previously soaking the cork discs in waste alcohol.

This type of mount permits direct examination of the genitalia both dorsally and ventrally. If the genitalia have been slightly tilted so that they lie on their lateral surface, the hole in the disc is still wide enough to permit examination of both dorsal and ventral surfaces. This method of mounting was satisfactory for the genitalia of *Conotrachelus*. A somewhat similar type was used by Mitchell (1936) for the preservation of the genitalia of *Megachile* (Hymenoptera). These mounts allow sufficient observation for taxonomic comparisons, but if detailed study is necessary, soaking the disc in xylene will dissolve the balsam and permit the removal of the genitalia.

Several dry mounts of genitalia were made, but with slightly softened genitalia and with genitalia that possessed a narrow apical process this method led to distortion of the specimen. The small vial-glycerine technique likewise could have been employed, but the balsam-filled cell mounts are easier to observe and more attractive in appearance.

A discussion of the technique involved in the eversion of the endophallus of the male genitalia is given on page 32.

## B. MEASUREMENTS

In measuring the various areas of the insect body and the male genitalia, the following system was employed: the length of the insect

was calculated from the anterior margin of the eye to the apex of the elytra, while that of the beak was a straight line from the apex to the ventral angle of junction between the beak and the eye. The length of the prothorax was computed dorsally at the midline, while the width was taken at the broadest point dorsally. The basal area of the elytra up to and including the humeri was the criterion for the elytral width, while the length of the elytra was calculated from the basal margin to the apex at the line of junction of the wing covers. The length of the aedeagus was measured dorsally from the basal median point to the apical median point, while the width was calculated only at the base. If the lateral plates of the aedeagus narrowly extended beyond the major portion of the base, as in *naso* Lec. (Fig. 59), the width was taken at the place where the narrow extensions of these plates joined the major basal portion of the aedeagus. The aedeagal struts were measured from their tips to their junction with the aedeagus.

### C. STUDIES OF COLLECTIONS AND TYPES

In order to get representations of the *Conotrachelus* fauna in the states included in this study, loans were requested of the universities and scientific societies in those states. In addition, requests were also sent to museums and to private collectors outside the midwestern area. The institutions and individuals from whom loans were secured are listed below. Other collections studied but not secured in loans are given; these are marked by an asterisk.

\*Blanchard Collection, Museum of Comparative Zoology, Cambridge, Massachusetts.

\*Bowditch Collection, Museum of Comparative Zoology, Cambridge, Massachusetts.

\*Casey, Greene, Soltau, and Wickham Collections, United States National Museum, Washington, D. C.

\*Dietz Collection, Museum of Comparative Zoology, Cambridge, Massachusetts.

\*Eddy Collection, Museum of Comparative Zoology, Cambridge, Massachusetts.

\*Fall Collection, Museum of Comparative Zoology, Cambridge, Massachusetts.

Field Museum of Natural History, Chicago, Illinois.

Frost Collection, Framingham, Massachusetts.

Hayes Collection, Urbana, Illinois.

Illinois State Natural History Survey, Urbana, Illinois.

Iowa Insect Survey Collection, Iowa Wesleyan College, Mt. Pleasant, Iowa.

\*Leconte Collection, Museum of Comparative Zoology, Cambridge, Massachusetts.

\*Liebeck Collection, Museum of Comparative Zoology, Cambridge, Massachusetts.  
Massachusetts State College, Amherst, Massachusetts.

Nason Collection, Department of Entomology, University of Illinois, Urbana, Illinois.

\*North Carolina State Department of Agriculture Collection, Raleigh, North Carolina.

University of Kentucky, Lexington, Kentucky.

University of Minnesota, St. Paul, Minnesota.

University of Missouri, Columbia, Missouri.

University of Wisconsin, Madison, Wisconsin.

To be certain of specific identities, the type specimens of Leconte, Walsh, and Fall, at the Museum of Comparative Zoology, Cambridge, Massachusetts, and those of Schaeffer and Casey at the United States National Museum, Washington, D. C., were examined. In some cases types were inaccessible, and in these instances careful checking of the descriptions and examination of specimens identified as these species by various coleopterous specialists were the criteria employed.

#### D. ORGANIZATION OF DISTRIBUTIONAL DATA

In the distributional data, all locality records are from specimens actually seen by the writer. No previous state records from catalogues or publications have been included because of the possibility that misidentifications may have occurred.

In the consideration of holotypes, allotypes, paratypes, lectotypes, etc., the present location of the specimen involved is indicated by the capital letters enclosed in parenthesis at the end of the statement. The key to these abbreviations is as follows:

- (MCZ).....Museum of Comparative Zoology, Cambridge, Massachusetts.  
(USNM) .....United States National Museum, Washington, D. C.  
(ISNHS).....Illinois State Natural History Survey, Urbana, Illinois.  
(WPH).....Private Collection of Professor W. P. Hayes, Department of Entomology, University of Illinois, Urbana, Illinois.  
(MSC).....Massachusetts State College, Amherst, Massachusetts.  
(PU).....Purdue University, Lafayette, Indiana.  
(IISC).....Iowa Insect Survey Collection, Iowa Wesleyan, Mt. Pleasant, Iowa.  
(CAF).....Private Collection of Mr. C. A. Frost, Framingham, Massachusetts.  
(UMo).....University of Missouri, Columbia, Missouri.  
(HFS).....Private Collection of H. F. Schoof, North Carolina State College, Raleigh, N. C.  
(UIDE).....University of Illinois, Department of Entomology, Urbana, Illinois.

### IV. THE MORPHOLOGICAL CHARACTERS OF TAXONOMIC IMPORTANCE

The following discussion of the important morphological characters used in the taxonomy of *Conotrachelus* is based only on the species included in this study. The discussion is divided into four sections: (A) the body regions and their appendages, (B) coloration and vestiture, (C) characters for sex determination, and (D) the male genitalia.

## A. THE BODY REGIONS AND THEIR APPENDAGES

In the head region the characteristics of the beak are of chief importance. The head capsule in the different species is similar, usually being densely punctured, with the punctures smaller than those of the thorax. The beak, on the other hand, shows variations not only in the different species but also in the sexes.

The most reliable specific character of the beak is its length and form, either of which varies greatly in many of the species. By means of the length and slenderness of the beak it is possible to distinguish the females of both *elegans* (Say) (Fig. 39) and *hayesi* n. sp. (Fig. 40) from the female of *aratus* (Germ.) (Fig. 41). In the female of *naso* Lec. the beak is extremely long, reaching the abdomen, and this character alone separates it from the female of *posticatus* Boh. where the beak only attains the mesocoxae. The curvature of the beak sometimes is more pronounced in one species than in another, as in *nenuphar* (Hbst.) and *hayesi* (Figs. 35 and 40). In some species, especially those of Group III, the curvature is slight until near the antennal insertion, where it is suddenly bent inwards.

Another beak characteristic of importance is the ratio of the distance between the lateral apical emargination of the beak and the anterior margin of the ball of the antennal scape to the distance between the dorsal and ventral surfaces of the beak at the position of the antennal insertion. (See Fig. 105.) This is especially evident in species whose beaks differ in stoutness, since this proportional character affords a method by which the terms stout and slender can be given a more concrete basis.

The sulci of the beak are of secondary importance in specific identification, being used more in sex differentiation. The beak usually has three lateral sulci on each side between the base and antennal insertion. These sulci have been called the upper sulcus, the median sulcus, and the lower sulcus, the latter being that sulcus nearest to the antenna. Occasionally the lower sulcus is divided into two as in *tuberosus* Lec. These sulci have been used in descriptions in the past, the usual reference being "strongly sulcate or striate," "deeply striate," or "feebly striate." These statements, however, are too inflexible, and many times fit only certain individuals of a species. Frequently the sulci are distinct in one specimen and feeble in another, they may vary in distinction on the different sides of the beak, or the basal half of a sulcus may be distinct, the apical half obscure. Consequently one must be cautious in diagnosing the type of the sulci; otherwise the characterization may lead to confusion. These sulci sometimes are not present as in *adspersus* Lec., and in this case their absence is an excellent diagnostic character. If the sulci are present, distinction between species based on the relative development of the sulci is not altogether reliable.

Other sculptural features of the beak such as punctation and carination are more significant for sex differentiation than for specific distinction. The prominence of a dorsal median carina is sometimes largely dependent on the development of the uppermost sulci.

The position of the antennal insertion on the beak is primarily a sex characteristic, but the relative length of the funicular segments of the antennae is sometimes of specific interest. In a majority of the species the first two segments are subequal in length and each is longer than any of the others. The apical segments generally tend to become successively globose, and the first, while subequal in length to the second, is frequently much stouter. The most notable exceptions to the above pattern are *adpersus* Lec. and *recessus* (Csy.) where the first funicular segment is approximately as long as the next two combined.

The characters of the prothoracic region are principally based on the sculpture of the dorsal and lateral areas. These areas show differences in punctation, carination, and tuberculation in the various species. The punctation in all cases is dense and varies from reticulate to cribrate. It is difficult to set up distinctions based on the size and form of the punctures, since many of the species have punctations which are quite similar; and while the differences are evident with the insects in juxtaposition, it is quite difficult to describe them so that the user of the key may identify a single specimen. The species *geminatus* Lec. and *cribricollis* (Say), however, differ so greatly in their punctation that they can easily be separated or identified by its use.

The prothorax is sometimes longitudinally carinate on its median, dorsal surface, and this character has been used much in the past for specific distinction. In some species such as *scniculus* Lec., *naso* Lec., *leucophaeatus* Fahr., and *posticatus* Boh., it is a stable characteristic, but in others like *affinis* Boh. it is unreliable. In *affinis* Boh., *nenuphar* (Hbst.), and *buchanani* n. sp. the carina may be distinct on the apical half in some individuals; in others it may be lacking. Until a long series of specimens is examined, the relative distinctness of a prothoracic carina cannot be considered a certainty.

Tubercles are also present on the prothorax, particularly in Group I. Usually there are two discal pairs, one transversely at the middle, the other between the median pair and the basal margin. The prominence of these protuberances, however, like the prothoracic carina, is subject to much variation. Consequently, it cannot be used for specific distinction. Nevertheless, one western species not considered in this study, *tuberculicollis* Schffr., has such large and prominent tubercles that they are valid specific characters.

The presence of a median furrow on the prothorax is one of the

characters used to separate Group III from Groups I and II. It may vary in prominence, but it is always evident.

The relative length and width of the prothorax is an aid in description, but not for specific identification. In all the species studied it was wider than long, but the ratio between the two dimensions was variable.

Ventrally, the prothorax is always provided with a groove for the reception of the beak. This character is of importance in subfamily and tribal classification.

The mesothorax has two structures of importance, the mesoscutellum and the mesosternum. The mesosternum has been used by Leconte (1876) and Blatchley and Leng (1916) in separating *geminatus* Lec. and *cribricollis* (Say) from *posticatus* Boh., the structure being considered prominent in the latter, and not prominent and sloping downwardly in the other two species. This characterization is ambiguous, however, since the mesosternum of *cribricollis* (Say) can be considered prominent and it definitely does not slope anteriorly as is true in *geminatus* Lec. The writer has used the same structure in the present classification, but has placed the emphasis on the basal angles.

The mesoscutellum is a new taxonomic character in *Conotrachelus* which was first noticed in working with *albicinctus* Lec. and *buchanani* n. sp. These two species, as will be noted in the key (p. 41), are separated by this character; the mesoscutellum in *albicinctus* Lec., when viewed from the lateral aspect, is abruptly declivent basally, while that of *buchanani* n. sp. slopes gradually toward the base (Figs. 29 and 30). The same character has also been used to distinguish *iowensis* n. sp. from *nenuphar* (Hbst.). Before this character is employed to differentiate other species, however, it should be checked in a number of specimens, since the shape of the mesoscutellum in some species is not always constant.

The metathorax is chiefly of importance in sex determination as explained on page 24.

The thoracic appendages are of much significance both as characters for sex determination and as specific indicators. With the elytra, the costate alternate intervals have been emphasized a great deal by Leconte (1876), Blatchley and Leng (1916), and Mutchler and Weiss (1925), and in several instances it appears that too much importance was placed on them. In those species where the costae of intervals 3 and 5 are interrupted to form abrupt elevations, as in *nenuphar* (Hbst.), *albicinctus* Lec., and others, the interruptions are distinct and constant in occurrence. In species, however, where those costal elevations are feeble, as in *elegans* (Say) and others, the interruptions occurring in the costa of interval 5 are feeble and extremely variable. For example: *elegans* (Say)

is described as having the costa of interval 3 twice interrupted and that of interval 5 "not interrupted posteriorly at the postmedian band," while *aratus* (Germ.) has the costa of interval 3 twice interrupted and that of interval 5 "not broken anteriorly." As these two species have been difficult to separate the obvious difference in the form of the costa of interval 5 has been logically seized upon as a specific character. Mutchler and Weiss (1925) incorporated this costal difference into their descriptive key of this genus. When various individuals of both of these species are examined, however, it is revealed that the costa of interval 5 in *elegans* (Say) is complete or once interrupted posteriorly, or occasionally feebly interrupted anteriorly, while that of *aratus* (Germ.) is usually twice interrupted, sometimes once anteriorly. Consequently, a distinction between the two species on the basis of the interruptions of the elytral costal of interval 5 is valueless. The writer has also found that the elytral costa of interval 5 in numerous other species of Group I varies in form to the same extent as it does in the previously mentioned species. Too much weight, therefore, should not be placed on the interruptions of the costa of interval 5 unless the character has been found constant in a long series of specimens. In five specimens of *hayesi* n. sp. the costa of interval 5 is only interrupted anteriorly, but the writer feels that in all probability future specimens will show variations.

The interruptions of the costa of interval 3 in contrast to those of the interval 5 are two in number and constant in occurrence in Group I, except in *falli* Blatch., *nivosus* Lec., and rarely *elegans* (Say). In Groups II-IV the intervals are sometimes non-costate, and when they are costate two strong interruptions of the costa of interval 3 occur only in *tuberosus* Lec. The elytral costae in these other groups are more stable in appearance than those of Group I.

Leconte (1876) stated that the elytral costae in *nenuphar* (Hbst.) are much more abruptly interrupted and the posterior elevations more prominent than in either *juglandis* Lec. or *albicinctus* Lec. This study has showed that while this is true in some instances, the reverse also occurs and, consequently, the relative abruptness and prominence of costal elevations are not to be relied upon.

In concluding this discussion of the elytral costae, it may be said that they are of distinct specific importance, but thorough observation should be made for any variations that may occur, before setting up a standard type for a species. Likewise, it should be kept in mind when identifying a specimen that a disagreement with the costal interruptions specified in the description should not be overemphasized if the other characters are in full agreement.

The humeri, serial punctures, relative length and width, and outline of the elytra are of special value in some species (e.g., humeri in

*crataegi* Walsh), but in general they are of less importance than the costae.

The legs are of much taxonomic importance. The number of teeth on the apical ventral area of the femora has been frequently used in classification. There are either one or two teeth present, the distal tooth sometimes being more of a denticle. These teeth usually are excellent characters, but a few intermediary species occur between the one- and two-toothed groups and confusion sometimes occurs. In those cases it has been necessary to insert a second character to clarify the situation. Thus, in *tibialis* n. sp. the male usually has the proximal tooth obliterated, and on this basis should go into the one-toothed group. Other characters and habitus, however, as well as the fact that the female has two distinct femoral teeth, place the species in the two-toothed group. Consequently, a tibial character of the male has been inserted in the key to prevent misidentification.

The punctuation of the legs has been studied, but it does not offer much possibility for taxonomic purposes, since it is similar in the majority of the species. The form of the tibiae, however, is of importance in some species, as in the male of *tibialis* n. sp. where the protibiae exhibit a remarkable distal concavity (Fig. 31a) in contrast to the normal protibiae found in all other species of *Conotrachelus* (Fig. 31b). Likewise *anaglypticus* (Say) shows a distinct concavity at the distal end of the metatibiae in the male (Fig. 32a) usually not found in other species.

The most reliable leg character revealed by this study is the shape of the metauncus, or metatibial spine (Fig. 20). Before discussing the taxonomic value of this character, it is necessary to consider the morphology of the structure. The term uncus (pl. unci) is taken from Marshall (1932) who states that it is a stout, curved hook developed from the outer apical angle of the tibia. Another spine developed from the inner angle of the tibia is called the mucro (pl. mucrones). Usually each of these types of spine is distinct, but the uncus tends to shift inwards, so that in some cases it appears to rise from the inner angle and resembles a mucro. This shifting occurs in *Conotrachelus* as will be seen in Fig. 20 where both an uncus and a mucro are present. The mucro appears to be absent in the male in many cases, but it is present in the female, although often obscured by a tuft of setae. The uncus, on the other hand, is always evident in both sexes and is of value both specifically and for sex determination. The unci in the females are always single, never dentate, but in the male the metaunci are frequently dentate. Consequently, in many of the species the sexes can easily be determined by an examination of the metaunci. Therefore, in many cases where a distinguishing character between species has been lacking, it has been found possible to differentiate the species by considering the sexes

separately. Thus in *elegans* (Say) and *aratus* (Germ.) where a great deal of specific confusion has arisen in the past, it was found that the males of the two species are distinct, in that those of *elegans* (Say) have both meso- and metaunci dentate while in *aratus* (Germ.) only the metaunci are dentate (Figs. 25 and 26). The females of the two species are distinguished by differences in the length, stoutness, and form of their beaks (Figs. 39 and 41).

The shape of the dentate metauncus is sometimes of value in separating the males of species, as in the case of *affinis* Boh. and *hicoriae* n. sp. (Figs. 23 and 24). Species do not always show differences in the form of the denticle on the metauncus, and this is indicative of affinities (Figs. 26, 27, and 28). The shape of the metauncus may possibly vary in the same species (Fig. 25).

The chief taxonomic feature of the abdomen is its punctation, which in this genus varies from sparse to dense and from fine to coarse. It is an excellent indicator in those cases where the differences in the density and distinctness of the punctation are extreme, such as in the separation of *retentus* (Say), *affinis* Boh., and *hicoriae* n. sp. from *elegans* (Say), *aratus* (Germ.), *tibialis* n. sp., and others. Too much stress should not be placed on minor variations, however, since these may occur within the same species when enough specimens are examined. The chief difficulty with the use of abdominal punctation, as well as that of other regions, is the use of relative terms which apparently must be employed to indicate the density and coarseness of the punctures. Terms such as "sparse" and "dense" are significant, but there is a wide range between these extremes which cannot be definitely characterized. In this paper, "dense punctation" means one similar to that shown in Fig. 33, while Fig. 34 illustrates a "moderately dense" punctation in the top half of the illustration and one slightly greater than moderate in the bottom half. The presence of a few widely scattered punctures is termed "sparsely punctured." The writer has attempted to limit the use of abdominal punctation to the specific descriptions unless the differences have been exceptionally distinct.

The coarseness of punctures varies even on the same segment, as will be seen in Fig. 34, and the range between a fine and a coarse puncture is much greater than that which occurs between the extremes of density. A definite standard to refer to a "coarse," "fine," or "semi-coarse" puncture could not be devised because the scale would necessarily vary with the size of the species. The coarseness of punctures, consequently, has not been employed in the keys unless the distinction was obvious.

In the descriptions, both density and coarseness of punctures have been used. The number and type of punctures frequently vary on the different sterna, and such comparisons appear to be of distinct value in

descriptions. The fifth abdominal sternum\* frequently has a tubercle on both sides of the middle on the apical third, but the prominence of these tubercles is variable and the character is not reliable (see page 90).

#### B. COLOR AND VESTITURE

In the genus *Conotrachelus* as in many other groups, coloration is usually an unreliable character. Freshly emerged specimens naturally have a lighter color than those in which the pigment has been fully developed. This is particularly evident in those species of *Conotrachelus* that have been bred from nuts, such as *retentus* (Say), *affinis* Boh., and *hicoriae* n. sp. Specimens collected in nature are much darker and at first glance would appear to be different from reared specimens. In a few cases, however, color is of importance, such as in *nenuphar* (Hbst.) and *iowensis* n. sp. where intense blackish areas on the elytra are characteristic of the species. In most of the species, the described piceous color may vary from black to red. Consequently, complete agreement between the color pattern of the specimen and that given in the description is sometimes lacking.

The type, density, and color of the vestiture are all of taxonomic importance as may be seen in the keys. The vestiture is usually composed of elongate, recumbent setae varying in color from white to a rusty red. These setae may be replaced by true scales, as in *recessus* (Csy.), or they may resemble scales to such an extent that they are termed "scale-like setae," as in *adspersus* Lec. Occasionally the prothoracic punctures and the elytral intervals bear, in addition to the recumbent setae, prominent suberect and erect setae, as in *cribricollis* (Say) and *erinaceus* Lec. The variations that occur in the type of setae present are innumerable, but the above are the principal forms.

The relative densities of the setae or scales in the different species are of much importance when these relations can be expressed so they are clearly evident to the user of the key who has only one specimen on hand. Only in those cases where differences in the density of the setae or scales are extreme are such characters used in the keys, as in couplet 1 of the Group IV key. In many of the species the setae are scattered about with small condensations here and there, but in Group I the species usually have a definite, postmedian condensation which is of use taxonomically both by its distinctness and by the color of the setae composing it (couplets 4, 5, and 7 of the Group I key).

The color of the setae varies considerably in the same species, but

\*The so-called fifth sternum is actually the seventh, since the first two abdominal sterna make up the posterior part of the metacoxal cavities and are not visible as sterna. The first visible abdominal sternum therefore is the true third. For taxonomic purposes and to avoid confusion, however, the true third sternum is considered the first ventral segment and the succeeding sterna are named accordingly.

there are several species in which the setal color is almost always constant in certain areas, such as in the postmedian bands of *buchanani* n. sp. and *albicinctus* Lec., and in the oblique, elytral bar of *anaglypticus* (Say).

The examples of the taxonomic value of the vestiture could be further enumerated, but a perusal of the keys and the descriptions, particularly the special characters, will indicate in a much better way its significance. The one disadvantage in its use is that specimens occasionally have their vestiture badly rubbed.

### C. CHARACTERS FOR SEX DETERMINATION

The sexes of all the species of *Conotrachelus* may be differentiated by the presence of an additional visible abdominal tergum in the male. Thus it will be seen in Fig. 10 (male) that the eighth tergum is distinctly evident, while in Fig. 12 (female) it is wholly concealed beneath the seventh tergum (shown by dash line). This sex character in *Conotrachelus* was discussed by Thomson (1932) for the sexes of *nenuphar* (Hbst.). The only possible disadvantage in the use of this character for the determination of the sexes is that it necessitates the disengagement of the elytra, but this is of little consequence when the sex of a specimen is an essential datum.

There are several other characters useful in sex determination, but none of these are common to the entire genus. Instead, they seem to occur at random among the different species. The first of these characters is the presence of dentate metaunci in the males of certain species. As the unci of all females are non-dentate, this character is a reliable one. It is found in some species of all the groups except Group III. In Group I dentate metaunci are more common than in the other groups, being found in *juglandis* Lec., *nenuphar* (Hbst.), *retentus* (Say), *affinis* Boh., *hicoriae* n. sp., *elegans* (Say), *hayesi* n. sp., *tibialis* n. sp., and *aratus* (Germ.). In Group II dentate metaunci occur in the males of *naso* Lec., *carinifer* Csy., and *posticatus* Boh., and possibly in *cribricollis* (Say). In Group IV *crinaceus* Lec. is the only species with this character. The dentate metauncus of *nenuphar* (Hbst.) was not noticed by Thomson (1932), although he did mention the extra large size of that uncus in comparison to the unci of the pro- and mesotibiae.

The second of the secondary sex characters is the presence in the males of metasternal grooves extending from the posterior border of the mesocoxae to the anterior rim of the metacoxae (Fig. 19). This character is confined to Group I, although not present in all of the species. *C. juglandis* Lec., *nenuphar* (Hbst.), *albicinctus* Lec., *retentus* (Say), *elegans* (Say), *aratus* (Germ.), and *buchanani* n. sp. possess these grooves, which are particularly distinct in the first three named species.

They are frequently feeble in *retentus* (Say), *elegans* (Say), and *buchanani* n. sp.

The third character is one commonly observed in Rhynchophora, in which the male has a shorter beak than the female. This is true in a number of species of *Conotrachelus*, but in many instances both sexes must be available before the difference can be seen. In *naso* Lec., *hayesi* n. sp., and *adpersus* Lec. the sexes may easily be distinguished without such recourse, since the difference in the length of the beak in the two sexes is pronounced (Figs. 37 and 40).

Another use of the beak in sex differentiation is found in its sculpture, which is generally more distinct in the male than in the female. In the males the lateral sulci extend from the base to near the antennal insertion, the dorsal carina is acute, and the punctuation of the dorsal surface distad of the antennal insertion is dense, while in the female the grooves are less distinct apically, the carina is sometimes scarcely evident, and the distal punctuation is sparse and fine. The sculpture is a relative character, and only occasionally can the sex be definitely identified by it. The best example of such an instance is found in *juglandis* Lec.

The position of the antennal insertion on the beak is also of importance in sex determination. The female invariably has the antennae inserted nearer the middle of the beak than the male, but the difference in most instances is so slight that it is only useful in a comparison of the sexes. Frequently, however, the difference is so great that the character can be applied to the one sex in the absence of the other; for example, in *recessus* (Csy.) the antennae are inserted at the middle of the beak in the female and at the distal third in the male.

The foregoing characters are those which have been found to occur in several species. In addition, there are several sex differentiation characters which are limited to one or two species, such as the costate first and second elytral intervals of the males of *naso* Lec. and *posticatus* Boh., the apical concavity of the male protibiae of *tibialis* n. sp. (Fig. 31a), and the distal emargination of the male metatibiae in *anaglypticus* (Say) (Fig. 32a).

#### D. THE MALE GENITALIA

1. *Morphology*: The male genitalia of Coleoptera were treated in a general way by Sharp and Muir (1912), who made a comparative study of various species in this order. In addition, Sharp (1918) published a preliminary note on the male genitalia of the Rhynchophora in which he discussed the various genital structures found in this group. Verhoeff (1896), Sharp (1920), Hopkins (1921), Kaston (1936), and others have investigated the genital morphology of either a single species or a genus. The only morphological study on the male genitalia of

*Conotrachelus* was that made by Sharp (1920) on *C. brevisetis* Champ., a tropical species.

In almost all the investigations since 1912 the terminology of Sharp and Muir (1912) has been followed. Kaston (1936) used it, and in addition discussed and tabulated the terms employed by other workers. Included in Kaston's work is the nomenclature of Snodgrass (1935), which is the terminology employed in this paper, except in those cases where structures are involved which Snodgrass did not consider. Snodgrass' terms are followed because they are applicable to the various orders of insects, and the author feels that a nomenclature which can be used in this manner is far superior to one which is limited to a single order. In those cases where structures are involved which Snodgrass did not consider, the terminologies of Sharp and Muir (1912) and Sharp (1918) have been followed. Occasionally new terms have had to be devised.

The male genitalia are contained within an invagination of the body wall distad of the eighth abdominal segment. The term phallus is used collectively, to designate all the parts of the external male genitalia. The principal structures which make up the phallus (Figs. 1, 3, and 8) are the first and second connecting membranes, spiculum gastrale, phallobase, aedeagus, endophallus, and appendages of these parts.

In the following discussion each of these structures except the connecting membranes will be considered individually. Unless otherwise stated, all data refer to *C. nenuphar* (Hbst.).

The first connecting membrane extends from the body wall to the phallobase (Figs. 8 and 9, dash line), while the second leads from the phallobase to the aedeagus (Figs. 8 and 9, dotted line). Sharp and Muir (1912) named these parts reversely, but Sharp later (1918) designated them as above. The first connecting membrane fits tightly over the strongly sclerotized aedeagus and frequently is difficult to discern. Dorsally the alimentary canal enters this membrane, while ventrally the conspicuous spiculum gastrale arises from it. The second connecting membrane is doubled upon itself when the aedeagus is in repose and may be triplicated proximad of the aedeagus depending on the position of the phallobase. This membrane in repose is seldom straight as shown in Fig. 8, but more often is creased or wrinkled. In copulation it straightens out and allows the aedeagus to be protruded. The second connecting membrane is usually closely applied to aedeagal struts.

The spiculum gastrale (Figs. 1 and 3) is a conspicuous, curved, sclerotized rod found on the ventral surface of the aedeagus arising from the first connecting membrane. Apically it is strongly curved, while basally it divides into two forks between which a heavy membrane extends to form a broad plate. From the inner angle of the forked base a

slender internal groove proceeds apically, where it evanesces. The spiculum gastrale extends beyond the basal portion of the aedeagus and varies in width from that shown in Fig. 3 to a slender elongate rod. The majority of the spiculi observed were of the widened type.

The spiculum gastrale is attached by muscles ventrally to the sclerotized triangular portions of the eighth sternum, and to the lateral walls of the eighth tergum (Fig. 3, muscles C). These muscles serve to hold the spiculum gastrale in place in the abdominal cavity during copulation. Two other sets of muscles attach to the spiculum gastrale, one at its widened apex (Figs. 3 and 8, muscles A) and the other at that edge of the base which is proximad of the phallobase (Fig. 3, muscles B). These two sets of muscles are apparently the retractors and the protractors of the phallobase, as will be seen by comparing Figs. 8 and 9. The retractor group, from the apex of the spiculum gastrale to the phallobase, appears to be a powerful set of muscles and possibly aids in the retraction of the aedeagus. The protractor set is composed of a much less dense mass of muscles which in some instances is difficult to see.

The phallobase (Fig. 1), (tegmen of Sharp and Muir, 1912), consists of a sclerotized ring bearing two dorsal lobes (epimeres). According to Sharp (1918) the phallobase may also be an incomplete ring in some Rhynchophora, but in *Conotrachelus* the ring is always complete. The phallobase in Rhynchophora usually is provided ventrally with a single basally directed strut, but in *Conotrachelus* the median ventral region never develops basally to the extent that it might be termed a strut (Fig. 3). Various forms of this development are shown in Figs. 13 to 18. The epimeres are difficult to discern unless the phallobase is pulled up over the aedeagal struts (Fig. 9). Their shape is quite similar in the species of Group I to that shown in Fig. 1, but in Groups II, III, and IV, they may be much more elongate. The phallobase, in repose, is usually situated at the base of the aedeagus, but in *seniculus* Lec. it surrounds the aedeagus one-third of the distance distad of the base. As previously mentioned, the phallobase is acted upon by two sets of muscles (Figs. 3, 8, and 9).

The most conspicuous structure of the male genitalia is the strongly sclerotized aedeagus. Sharp and Muir term this structure the median lobe and consider the aedeagus as consisting of both the tegmen (phallobase) and the median lobe (Figs. 1, 2, and 8). The aedeagus is essentially a hollow tube inside of which the endophallus is contained. It varies greatly in form in the different species and is the most important structure for specific classification. Dorsally it consists of a pair of heavy sclerotized lateral plates and a median area. This median area when slightly sclerotized as in *nenuphar* (Hbst.) (Fig. 1) is termed the dorsal plate; when entirely membranous as in *naso* Lec. (Fig. 59) the dorsal

membrane. When a dorsal plate is present it is separated apically from the lateral plates by membranous areas (Figs. 1 and 52) except in *seniculus* Lec. (Fig. 56). These membranous areas, of course, are absent in those species having a dorsal membrane (Fig. 58). In either case the lateral plates, which also extend to the ventral surface, unite apically to form either a prominent process (Figs. 53, 66, 67, and 68), a feeble process (Figs. 42 and 50), or sometimes no process at all (Figs. 56 and 63). The dorsal areas of the lateral plates in Group I, particularly beyond the extent of the dorsal plate, become depressed so that subapically the lateral plates are solid dorsoventrally instead of the dorsal and ventral surfaces being widely separated. This may be seen by noting the gradual subapical convergence of the dorsal and ventral surfaces in Figs. 74, 78, and 79. Basally the lateral plates may unite (Figs. 52, 59, 62, and 64) or be separated by a dorsal membrane (Figs. 66 and 68) or a dorsal plate (Fig. 45). Frequently, as in Figs. 42, 46, 47, and 51, there is a faint internal indication of the extension of the dorsal plate to the base. The extent and shape of the dorsal plate and dorsal membrane are quite variable as will be seen by a comparison of Figs. 42 to 68. Neither of these structures extends to the apical junction of the lateral plates; instead each terminates a short distance before the junction.

Ventrally, the aedeagus is bounded by the same lateral plates, and the median area here also may be either lightly sclerotized (ventral plate) or membranous (ventral membrane) or both (Fig. 2). Usually the basal portion of the aedeagus is lightly sclerotized and the apical portion membranous, although the relative proportion of each type is variable (compare Figs. 84 and 85). In a lateral view the ventral membrane is usually the only portion visible.

On their ventral surfaces the lateral plates are extended basally in the form of two elongated projections (Fig. 2) which are termed aedeagal struts (median struts of Sharp, 1918, p. 217). These struts are always present in Rhynchophora and assume a variety of shapes and sizes. The same is true in the genus *Conotrachelus*, although in closely related species they differ but little. In *seniculus* Lec. the aedeagal struts are small, the aedeagus being eight and one-half times their length, while in *crataegi* Walsh the struts are three-fourths as long or may even equal the aedeagus in length. The apices of the struts also vary in form. The ventral plate likewise projects basally to give rise to an angulate structure between the aedeagal struts. This median projection is usually difficult to discern, since the second connecting membrane encircles it. Usually the projection extends beyond the basal border of the aedeagus, but occasionally it may be parallel to it as in *seniculus* Lec.

As previously mentioned, the dorsal plate or membrane does not extend to the apical junction of the lateral lobes, so that there remains

distad of it an area in which the ventral membrane is visible from above. Since this area is distad of the phallotreme (Fig. 5), it has been termed the prephallotremic area (Figs. 1 and 42).

Summarizing, it may be said that the aedeagus is a hollow structure consisting of two heavily sclerotized lateral plates which extend both dorsally and ventrally and are separated dorsally and ventrally by median, membranous, or lightly sclerotized areas.

The endophallus (Figs. 4 and 11), (internal sac of Sharp and Muir, 1912; praeputial sac of Verhoeff, 1896), is that structure of the male genitalia which effects the transfer of sperm from the male to the female. It bears the opening of the ejaculatory duct, the gonopore (Fig. 7), (functional orifice of Sharp and Muir, 1912), and is instrumental in bringing about a close connection between this orifice and the mouth of the spermathecal duct in the female. The endophallus is chiefly membranous, but also contains sclerotized plates as well as numerous spines. When not in use in copulation, it is usually inverted and contained within the aedeagus (Fig. 4) with the sclerotized, lateral plates of the aedeagus on the sides, the dorsal plate above, and the ventral plate and membrane below. In such a position the endophallus occupies the greater portion of the aedeagal cavity. Usually it remains in this position until the aedeagus is inserted into the female during copulation, but in some species of *Lucanidae*, *Heteroceridae*, *Lycidae*, and *Scarabaeidae* (Sharp and Muir, 1912, p. 607) the endophallus is permanently everted and is never contained within the aedeagus. Thus it appears that the principal functions of the aedeagus are to place the endophallus in a position where it can effect a close connection between the sperm duct of the male and the spermathecal duct of the female, and to protect it while copulatory attempts are being made.

In *C. nenuphar* (Hbst.) the endophallus (Figs. 7 and 11) consists of two large, sclerotized, roughly diamond-shaped plates and a membranous portion which makes up its greater area. The membranous area is covered with numerous spines and is trilobed when fully everted. The lateral, membranous lobes are broad basally and narrowed apically, the spines becoming larger as the lobes narrow. When everted the lateral lobes push out to the sides and curve basally. In this position they doubtlessly function as a holding mechanism in copulation. The middle lobe is directed apically and consists of a broad, dorsal lobe and an elongate, ventral lobe. The dorsal lobe is separated from the lateral lobes by minutely spined or spineless strips, while the ventral lobe is ventrad of the lateral lobes. In repose the ventral lobe hangs beneath and to the side of the main portion of the endophallus (Figs. 4 and 5). In this position, it may be seen to contain many internal spines, all of which are directed apically. The ventral lobe of the endophallus is extremely diffi-

cult to evert even in fresh specimens, and only after repeated efforts is extension successful. The dorsal lobe, in comparison, everts readily and may be fully extended even though the ventral lobe is still within the aedeagal cavity. Because of this arrangement of the two lobes, and the fact that when forced out of the aedeagal cavity by vigorous pulling with a needle, the ventral lobe hung limply beneath the dorsal lobe, it was at first concluded that the ventral lobe was incapable of protrusion. The presence of a strongly spinose, internal wall in a passive structure, however, appeared to be a paradox. Up to this time, attempts to evert the ventral lobe had been on the assumption that the lobe was a tubular structure which would evert by a reversal of the internal and external walls such as occurs in the dorsal lobe (compare Figs. 5 and 11). The ventral lobe, though tubular in outline in repose, does not extend in this manner. The tubular outline of the lobe is brought about by a pushing in of the dorsal wall so that a double-layered tube is formed (Fig. 6a). In this way the spines which are present on the lateral edges at the apical tip of the ventral lobe (Fig. 7) approach each other as shown in Fig. 6a. In repose, the tube thus formed has the spines internally and pointing apically. When eversion takes place, the inner spinose layer is thrown upward and laterally (Figs. 6b and 7) and the spines are directed basally. When so extended, the ventral lobe appears to be an accessory holding mechanism for use in copulation. The location of the gonopore between the two sclerotized plates (Fig. 7) instead of at the tip of the ventral lobe would further indicate this type of function for the ventral lobe. The lobe has muscles attached to its apical end which serve for its retraction and possibly aid in the inversion of the entire endophallus.

Although mechanical eversion of the ventral lobe was possible in fresh specimens, the genitalia of one male killed when in copulation showed the ventral lobe within the aedeagal cavity although the remainder of the endophallus was fully everted. This, plus the extreme difficulty of everting the ventral lobe, leads one to the conclusion that the lobe possibly does not extend during copulation but has a more passive role.

When the endophallus is everted the two sclerotized plates lie proximad and dorsad of the membranous portion (Figs. 7 and 11). These plates form the transfer apparatus (Sharp, 1918, p. 218), and are of great importance since the ejaculatory duct has its opening between them. Both plates are roughly diamond-shaped, and each contains a hole, the purpose of which is not apparent. Attached to the plates are muscles used to retract the endophallus, while lying between the plates is the small, obscure opening of the ejaculatory duct, or gonopore. Dorsad and proximad of the transfer apparatus is a small, slightly sclerotized plate having teeth along its apical border (Figs. 7 and 11, hinge plate). This

structure is attached to the dorsal plate of the aedeagus and serves as a hinge upon which the endophallus is everted. When the endophallus is in repose the sub-basal edge of this hinge plate projects beyond the apex of the dorsal plate of the aedeagus (Figs. 4 and 5). The opening beneath the hinge plate formed by the inversion of the endophallus is termed the phallotreme (Fig. 5).

The natural eversion of the endophallus is effected by blood pressure (Sharp and Muir, 1918, pp. 610-11). This phase of the eversion was not studied by the writer, the method of eversion being considered primarily. The points mentioned in the following discussion were determined by artificial eversion of the endophallus with a needle, but the writer feels that the normal method would be the same regardless of the difference in the agent.

In repose, the endophallus is as shown in Figs. 4 and 5. The dorsal plate of the aedeagus is level with the lateral plates (Fig. 9), the dorsal lobe is inverted with its spines on the inner wall, the lateral lobes approach each other apically, diverging basally where they pass beneath the transfer apparatus. The latter is most evident, being in the approximate central area of the entire sac and just beneath the dorsal plate. The hinge plate has its spines pointing basally and its basal border protruding distad of the apical edge of the dorsal plate. The ventral lobe has its apical end projecting beyond the basal border of the aedeagus beneath the second connecting membrane (Fig. 4, connecting membrane not shown), and the ejaculatory duct may be seen rising from near the ventral membrane of the aedeagus and passing dorsally over the sac to its insertion between the plates of the transfer apparatus (Fig. 5). The courses that these various structures follow during the eversion of the endophallus are shown diagrammatically in Fig. 5 and are also evident by comparison of Figs. 4 and 7. The lateral lobes slowly push out toward the sides, curving basally, while the dorsal lobe area slowly everts apically. At the same time, the hinge plate and the plates of the transfer apparatus swing ventrally so that their basal point shown in Fig. 4 becomes their apical point in Fig. 7. The reversal of these plates requires an increase in the size of the phallotreme (median orifice of Sharp and Muir, 1912, p. 482), and this is accomplished by the elevation of the dorsal plate of the aedeagus (Fig. 11). Extension of the ventral lobe, if occurring, takes place after the lateral and dorsal lobes and transfer apparatus have been fully everted. The complete eversion finds the structures as shown in Figs. 7 and 11, the endophallus presenting an approximately forty-five degree slope.

Sharp (1920, Plate IV) found the endophallus in *Conotrachelus brevisetis* Champ. (a South and Central American species) when everted

to consist of a large ventral bladder-like sac with a distinct small lobe containing the transfer apparatus on the dorsal surface of its base. Sharp considered this position of the transfer apparatus as remarkable, since these plates are usually more closely connected with the wall of the main sac and placed more or less at its apex. In *C. nenuphar* (Hbst.) a dorsobasal position of the transfer apparatus is obtained, but the apparatus is not set off in a small lobe from the remainder of the sac. Sharp also stated that the extreme hardness and complex shape of the transfer apparatus in *C. brevisetis* Champ. was unusual in the Curculionidae. The writer, although not making a detailed study of the endophallus in other species of *Conotrachelus*, has noted that a complex, hardened, transfer apparatus does occur in a number of species, such as *seniculus* Lec., *cribricollis* (Say), *leucophaeatus* Fahr., *naso* Lec., *posticatus* Boh., *fissunguis* Lec., *anaglypticus* (Say), *crinaceus* Lec., *crataegi* Walsh, *geminatus* Lec., *tuberosus* Lec., and *adspersus* Lec. In these species, excepting *seniculus* Lec., the transfer apparatus consists of one to three pairs of sclerotized bars. These bars assume a variety of shapes, some being J-shaped, others elongate and sinuate, and still others semicircular. In some instances the bars protrude into the prephalлотremic area as is shown in Figs. 59, 60, and 68.

The technique of artificial eversion of the endophallus is simple to explain but difficult to apply. After removal, the genitalia are held in place by a small needle pushed through the phallobase. Since the endophallus apparently does not attach below to the ventral membrane but is suspended from the lateral plates, a fine needle with a slightly hooked end is then inserted between the ventral membrane of the aedeagus and the endophallus with the hook turned sidewise. When the needle passes the basal end of the endophallus, it is twisted so that the hook points dorsally. It is then slowly withdrawn, and if a hold on the endophallus has been obtained, eversion is gradually accomplished. Usually, several attempts have to be made before success is attained. In this study fresh specimens were used, and the extension of the endophallus was not so difficult as it would have been in preserved specimens.

Sharp and Muir (1912, pp. 483-484) and Sharp (1918, pp. 220-221) described this method of eversion and their study was made on a wide range of Coleoptera with dried specimens up to sixty years of age. When eversion is complete, these workers inject the endophallus with water to restore it to its natural form. The smaller the specimen, the more exacting is the eversion, and in some cases it appears impossible. Specimens that have been killed and preserved in alcohol are not suitable for the extension of the endophallus (Sharp, 1918, p. 221). Specimens which are killed in alcohol and immediately examined, however, give suitable re-

sults. In fresh specimens of other Coleoptera, such as Staphylinidae, the endophallus may be everted by gently pressing upon the median lobe (Sharp and Muir, 1918, p. 483).

2. *Taxonomic Value*: The male genitalia are of distinct taxonomic importance in the genus *Conotrachelus*. Barber (1919, 1923), however, has been the only worker to use these structures in the taxonomy of this group. He separated males of *serpentinus* (Klug), *aguacatae* Barber, and *perseae* Barber by means of aedeagal differences. As the various structures of the male genitalia are not of equal significance, a brief discussion of their relative taxonomic values is given here.

The two connecting membranes are similar in all the species studied, and the spiculum gastrale appears to be affected by the age of the individual, so that these three structures are of little taxonomic value.

The phallobase, on the other hand, shows some evidence of being useful, perhaps in the separation of groups of species, since it was noted that the epimeres usually are distinctly longer in Groups II, III, and IV than in Group I. There are also differences in the configuration of the phallobase, but in many instances closely related species have phallobases of similar form. In addition, the sclerotization of the phallobase varies within some species, and sometimes its limits are difficult to discern, so that it is not useful in classification. Originally the writer had some hope that the median, ventral area might be of use, since this area is wider than the remainder of the phallobase and is produced basally in various shapes. It was found, however, that this median area varied greatly in form within some species (Figs. 14, 16, and 17), and frequently different species had similarly shaped, basal productions (Figs. 13 and 16).

The endophallus is of importance in the definition of groups of species and may be of specific value. In Group I, with the exception of *seniculus* Lec. and *nivosus* Lec., all the species have the same type of endophallus as that shown in *nenuphar* (Hbst.) (Figs. 7 and 11), although in some species it may be slightly modified. Essentially, however, it is the same even though the aedeagi of the various species may differ greatly in form (Figs. 42 to 54). In addition to these aedeagal differences, the external morphological characters of the species are also variable, as will be noted by a brief glance at the descriptions of some of the species in Group I. From this, one may infer that the endophallus is a true index to group relationship even when the other morphological characters of the species are divergent. This relationship is mainly evident by examination of the transfer apparatus which is the prominent sclerotized part of the endophallus (Fig. 7). Sharp (1920, p. 75) states: "The shape and nature of the transfer apparatus differs greatly in the various forms of Rhynchophora, so that it will be difficult to generalize it for the purpose of

definition of the great groups, but it will be found very important in the case of definition of genera and tribes."

The endophallus may possibly be used as a specific character in those species which have a dorsal membrane instead of a dorsal plate (Figs. 58 to 62 and 64 to 68) and possess several distinct sclerotized bars in the transfer apparatus. When a dorsal membrane is present, the transfer apparatus is visible from above, and the size and shape of prominent sclerotized rods can be observed. Some of the less distinct bars, however, are obscure, so that the true relationship of all the structures in the transfer apparatus cannot be determined unless the endophallus is everted. In the descriptions of the male genitalia of *cribricollis* (Say), *geminatus* Lec., and other species of Groups II, III, and IV, mention is made of the shape and position of the prominent bars of the transfer apparatus. The sclerotized bars, when beneath the dorsal membrane, are not shown in the illustrations, since, without being everted, their relationships could not be accurately determined. When the sclerotized bars protrude into the prephallotremic area, they are included in the illustrations (Figs. 59 and 60). A specific difference in the sclerotized bars of these two species is clearly perceptible. The greatest handicap to the use of the endophallus is the difficulty of its eversion, even in fresh specimens. If this handicap is ever overcome, a distinct advance in the phylogeny and taxonomy of this genus will be possible.

The genital structure of the most taxonomic significance is the heavily sclerotized aedeagus. The aedeagus shows distinct variations among the different species and yet is constant within a species. There are minor variations in size and shape within a species, as will be seen by comparison of Figs. 1, 4, and 7, but these variations are too slight to prevent the use of the aedeagus in specific identification. A series of eleven specimens of *seniculus* Lec. from the same locality were examined to determine the extent of variation in such a group, and specimens from other localities were also examined. Some slight variations in the dorsal outline were found. In some instances an evident indentation was present at the apical third instead of only a feeble indication as shown in Fig. 56. The lateral plates and dorsal plate also varied slightly in their relative proportions. In no case, however, were the variations such that the aedeagus could be mistaken for that of another species. Numerous specimens of *nenuphar* (Hbst.) were also examined, and a similar conclusion was drawn.

The specific variations of the aedeagus are illustrated in Figs. 42 to 95. Before discussing the relative value of the parts of the aedeagus, it is necessary to define some of the terms not yet discussed. In a dorsal view, the outer limit of the lateral plate, on each side, is termed the outer curvature (Fig. 42). The inner limit is termed the inner curvature

(Fig. 42). From the lateral aspect the upper boundary of the lateral plate is designated the dorsal curvature; the lower boundary, the ventral curvature (Fig. 84).

In a dorsal view of the aedeagus the outline of the structure is of utmost importance. For example, its shape in *aratus* (Fig. 53) is distinctly different from that in *elegans* (Fig. 51). All other species also differ in this respect. The inner curvature is of less importance, but varies in the different species, as will be seen by a comparison of Figs. 61, 64, and 67. Sometimes this curvature is rather indistinct basally, as is shown in Figs. 60 and 65 (irregular lines).

The dorsal plate varies in shape in the different species, but it also may vary quite extensively in the same species. Unless the dorsal plate is exceptionally distinctive, as in *aratus* (Germ.) (Fig. 53) and in *crataegi* Walsh (Fig. 57), it is not a reliable character. The presence of the dorsal plate links together all the species of Group I in contrast to those of Groups II, III, and IV, where a dorsal membrane replaces the plate (except in *crataegi* Walsh). Another distinctive group feature is that the apex of the dorsal plate is usually transverse (Figs. 42 to 54) while that of the dorsal membrane is either V-shaped or semicircular apically (Figs. 62 and 68). Exceptions to these generalizations are found in *crataegi* Walsh (Fig. 57) which has a dorsal plate that is V-shaped apically, and in *seniculus* Lec. and *hayesi* n. sp. which have the dorsal plate incurved apically.

In *seniculus* Lec. the dorsal median area is lightly sclerotized, but no membranous areas are present between the dorsal plate and the lateral plates as in the other species (except *nivosus* Lec.) of Group I. Another aberration in Group I in regard to the structure of the dorsal median area is found in *nivosus* Lec. where the dorsal plate is obliterated except for a minute triangular piece basally. It may seem from this discussion that there are so many exceptions that no definite relationships are present. If it be remembered, however, that numerous southwestern and Gulf Coast species are not considered in this study, then these discrepancies in the data are explained in part. The writer believes that with a larger series of species the presence of a dorsal plate or membrane and its various intermediate and aberrant shapes may be successfully explained phylogenetically.

The dorsal plate usually is difficult to see in glycerine or alcohol mounts unless the endophallus is everted or unless it is heavily sclerotized, which is rarely the case. If the aedeagus is allowed to dry temporarily, the dorsal plate becomes distinct. When in a liquid mount, considerable manipulation is necessary before its shape can be observed.

The apical process is variable in its development in various species (Figs. 42, 43, 47, 53, 54, 60, and 62). When a process is present, it is

easy to distinguish between the species, such as in Group I, where *nenuphar* (Hbst.) by the possession of a distinct apical process is readily distinguished from its close relatives, *buchanani* n. sp., *iowensis* n. sp., *juglandis* Lec., and *albicinctus* Lec. (Figs. 42 to 46). The shape of the process is also of value, as will be noted with the species of Group III (Figs. 66, 67, and 68). Since the apex of the aedeagus is curved ventrally, it is not visible in the dorsal view. Consequently, a separate sketch of the apex in the various species has been made to show its form and prolongation (Figs. 42 to 68).

The aedeagal struts do not vary significantly in closely related groups and are not included in the illustrations.

The lateral view of the aedeagus (Figs. 69 to 95) is chiefly important for the observation of the dorsal and ventral curvatures. Usually it is less important than the dorsal view. The lateral plates, dorsal plate or membrane, and the ventral plate or membrane are visible in a lateral view.

The dorsal plate or membrane varies in its prominence depending on whether or not the endophallus is slightly everted. Sometimes it is quite prominent (Figs. 74 to 77), at other times scarcely evident (Figs. 72 and 73). The ventral plate is visible in only a few species (Figs. 84, 85, 86, and 87), but the ventral membrane is usually evident. The dorsal and ventral plates or membranes, however, are usually not of taxonomic importance in a lateral view, since they vary greatly, depending on the position of the aedeagus and the extent to which the endophallus is inverted. These two structures are included in the drawings chiefly to orient the lateral position of the aedeagus so that comparisons with the illustrations may be made from specimens in the same position. The dorsal and ventral curvatures vary in the different species and are of distinct importance. Comparison of Figs. 86, 87, 91, and 92, as well as the other lateral figures, will illustrate this point.

An interesting point concerning the aedeagi is that their length may not be in proportion to that of the adults. Thus the aedeagus of *hayesi* n. sp. (Fig. 52) is distinctly longer than that of *juglandis* Lec. (Fig. 42), although the adults of the *hayesi* n. sp. range from 4.7 to 5.1 mm., and *juglandis* Lec. from 5.9 to 7.1 mm. The same is true of *recessus* (Csy.) (Fig. 63) and *tuberosus* Lec. (Fig. 66), although the adults of both have the same range in length.

It appears from this study that excepting those morphological characters on which Groups I to IV are based, the genitalia (aedeagi) are truer indicators of specific relationships than the external morphological characters. Thus, in Group I the aedeagus of *falli* Blatch. clearly shows that it belongs in the group with *nenuphar* (Hbst.) and *elegans* (Say), even though its elytral and prothoracic sculpture is greatly different from that of these species. In Group III, *tuberosus* Lec. has the elytral costae

similar to those of *nenuphar* (Hbst.), yet its aedeagus (Fig. 66) clearly shows that it is related to *anaglypticus* (Say) and *leucophaeatus* Fahr. (Figs. 67 and 68). The close affinity of *fissunguis* Lec. and *erinaceus* Lec. is also evidenced by similarities in their aedeagi (Figs. 64 and 65), even though externally they are very distinct. The aedeagi in these instances indicate that the basic characters on which the groups are erected are valid, and do not fluctuate as do other previously mentioned "superficial" characters.

## V. NOMENCLATURE

The principal nomenclatural question in this genus involves the authorship and the position in the Curculionidae of the generic name *Conotrachelus*. Schönherr (1837 and 1845), Agassiz (1842-46), Lacordaire (1866), Provancher (1877), and Scudder (1882) credit Latreille (1835 or 1837) with the name *Conotrachelus*, while Melshheimer (1853), Gemminger and Harold (1871), Crotch (1873), Leconte and Horn (1876), Austin (1880), Champion (1904), Blatchley and Leng (1916), Leng (1920), Sherborn (1925), Schulze *et al* (1929), Hustache (1936), and Neave (1939) cite Schönherr (1837) as the author of the name. Dejean (1835, p. 296, and 1837, p. 321), who first published the name *Conotrachelus*, appended Latreille's name to it, and this has led some authors to credit Latreille with the generic name. Latreille, however, did not publish anything concerning the genus *Conotrachelus*, and consequently cannot be considered as its author. Schulze *et al* (1929) and Neave (1939) list *Conotrachelus* Dejean as a *nomen nudum*, but as Dejean first published the name and listed seventy-one species (i.e., names) under it, he may be considered as its author if any of the included specific names are valid. Of the seventy-one species listed by Dejean, four are considered valid by the writer. Two species, *concentricus* (Oliver) (1807) and *irroratus* (Fabricius) (1801), have definite bibliographic citations. The status of the other specific names, *diaconitus* Germar and *serpentinus* Germar, however, may be considered questionable by some in light of the strictest interpretation of the International Rules of Nomenclature. The facts concerning these names are as follows: Dejean (1835 and 1837) and Boheman (in Schönherr, 1837) both credited *Conotrachelus diaconitus* and *C. serpentinus* to Germar, but Germar did not describe either of them. Boheman included under his diagnosis of each of these species (pp. 397 and 402) this synonymy:

Conot. id. Dejean Cat. Col. ed. 2. p. 297, ed. 3. p. 321.

Balaninus id. Dom. Germ. in Litteris, teste Dom. Schuppel.

The first citation in this synonymy refers to Dejean's placements of 1835 and 1837, while the second apparently has reference to Boheman's

knowledge, or at least his belief, that the two species known to contemporary workers as *Balaninus diaconitus* Germar and *B. serpentinus* Germar were the same as the two placed in *Conotrachelus*, under the same two specific names, by both Dejean and Boheman. Klug (1829) briefly described *Balaninus diaconitus* and *B. serpentinus* and listed Germar (in lit.) as the author of both names. Klug's placement of Germar as the author of these names evidently was done only in deference to Germar, since the latter never published anything in connection with the two species. Consequently, Klug, being the first to publish the two names in connection with descriptive statements, must be considered as their author.

The question of the validity of these two names in the Dejean Catalogue depends on the interpretation of the previously mentioned data. If it can be inferred that Dejean (1835) had reference to *Balaninus diaconitus* (Klug) and *B. serpentinus* (Klug) when he included under the new genus *Conotrachelus* the specific names *diaconitus* Germ. and *serpentinus* Germ., then these two names can be considered valid in the Dejean Catalogue. The writer, basing his conclusion on three evidences, believes that such an inference can be made.

First, it would appear from Boheman's (1837) synonymy that Klug's (1829) species, *Balaninus diaconitus* Germ. (in lit.) and *B. serpentinus* Germ. (in lit.), Dejean's (1835) *Conotrachelus diaconitus* Germ. and *C. serpentinus* Germ., and Boheman's (1837) *C. diaconitus* Germ. and *C. serpentinus* Germ. are the same pair of species. Dejean and Boheman, as well as Klug, accepted Germar as the author of these species even though by present-day technical standards Klug himself was the author; similarly, as has been previously shown, Dejean and others accepted Latreille as the author of *Conotrachelus*.

The second evidence is found in the fact that in the Dejean Catalogue the two specific names are in the same consecutive order as they are in Klug's paper. This possibly is a coincidence, but it may also be an indication that Dejean was actually concerned with the Klug names at the time he erected the new genus *Conotrachelus*.

The third evidence is that it seems unlikely that Dejean would publish the same two specific names and ascribe to each the same author as Klug had done unless he was aware of Klug's paper and knew that the species (*diaconitus* and *serpentinus*) therein placed in *Balaninus* were the same as those which he (Dejean) placed in *Conotrachelus* under the same two specific names. It is quite probable that Dejean, Klug, and Germar had even had correspondence (or exchange of specimens and opinions), directly or indirectly, in regard to the two species in question. On this and the two preceding evidences the writer bases his conclusion that the names *Conotrachelus diaconitus* Germ. and *C. serpentinus* Germ.

as given in the Dejean Catalogue (1835) represent valid species, either of which is available as the genotype.

Two of the species originally included under *Conotrachelus* by Dejean have since been removed to another genus. Schönherr (1837, pp. 467 and 468) made *irroratus* (Fab.) the type of a new genus *Peridinetus*, and Chevrolat (1876, p. 229) placed *concentricus* (Oliv.) in the same genus. Both of these species are Barinae, and their removal from the Cryptorhynchinae is correct. Before seeing Klug's paper the writer believed *irroratus* (Fab.) and *concentricus* (Oliv.) to be the only valid species of *Conotrachelus* in the Dejean Catalogue. Under such circumstances the name *Conotrachelus* would be shifted to the Barinae, and the unfamiliar synonym, *Cyphorrhynchus* Schönh., would take its place. Fortunately the Klug paper of 1829 was called to the writer's attention by Mr. L. L. Buchanan, and a consideration of the validity of two other specific names, *diaconitus* Germ. and *serpentinus* Germ., became possible. This consideration has made it possible to retain the name *Conotrachelus* in the Cryptorhynchinae, a retention which is highly desirable in view of the well-known concept built around this generic name.

The type of the genus *Conotrachelus* Dejean is *diaconitus* (Klug), designated by Schönherr (1837, p. 392) as *diaconitus* Germ. The present synonymy of the genus is as follows:

*Conotrachelus* Dejean, 1835, Cat. Col., ed. 2, p. 296.

*Cyphorrhynchus* Schönh., 1837, Gen. Spec. Curc., IV, pt. 1, p. 458.

*Glycaria* Pascoe, 1880, Ann. Mag. Nat. Hist. (5) VI, p. 181.

*Edesius* Pascoe, 1881, Ann. Mag. Nat. Hist. (5) VII, p. 305.

*Loceptes* Casey, 1910, Can. Ent. XLII, p. 130.

The nomenclature of the species, when considered, is discussed under the individual species in the following section.

## VI. CLASSIFICATION

The genus *Conotrachelus* Dejean belongs in the family Curculionidae, subfamily Cryptorhynchinae, and tribe Ithyporini. It is characterized as follows: prosternum grooved, the groove never extending to mesosternum; head not transversely sulcate but with a fovea or feeble depression separating head and beak; antennal funicle with seven segments sparsely clothed with recumbent and suberect pale setae, suberect setae longer and arranged in whorls; prothorax with distinct postocular lobes; ornamental setae or scales present on prothorax and elytra, the latter with intervals 3, 5, 7, and 9 frequently costate, the costae of intervals 3 and 9 meeting apically; femora with one or two teeth on apical ventral surface, tibiae with distinct unci, tarsal claws usually divergent, sometimes approximate, toothed or cleft; fifth abdominal sternum with a small

tuft of pale, erect setae arising from apical third on each side of middle; aedeagus consisting of two heavily sclerotized lateral plates bordering dorsal and ventral median areas which are lightly sclerotized or membranous.

The species of this genus were separated into six groups by Leconte and Horn (1876) and Blatchley and Leng (1916). In the present classification only four groups are designated. These groups are erected not only for convenience of treatment, but also to exhibit the phylogenetic relations of the species more clearly.

Each species is described or redescribed on both the external morphological structures and the male genitalia. The redescrptions of previously described species are necessary because older descriptions omitted many of the characters now in use and several of them were based only on one sex. The citations under each specific name are those which have included descriptions of the species. Characters mentioned in the keys and diagnoses (special characters) are usually not repeated in the specific descriptions. Each description is followed by a brief discussion of the distribution, biology, phylogeny, or nomenclature of the species involved. The present locations of the type specimens are indicated by the capital letters inclosed in parenthesis at the end of the type citations. The explanation of these abbreviations is on p. 16. A brief glossary is given on p. 142.

#### KEY TO THE GROUPS OF CONOTRACHELUS

1. Tarsal claws divergent..... 2
- 1- Tarsal claws approximate.....Group IV, p. 129
2. Dorsum of prothorax without a median longitudinal furrow; apical half never with a longitudinal ridge on each side of the middle..... 3
- 2- Dorsum of prothorax with a median longitudinal furrow on the apical half; furrow bordered on each side by a longitudinal ridge; ridges and furrow sometimes feeble; if so, specimens will have an oblique bar of yellowish vestiture behind each humerus.....Group III, p. 118
3. With two femoral teeth, rarely one absent; if only the distal femoral tooth is present, the protibia will be distinctly concave apically (Fig. 31a), or, if the proximal tooth is distinct and the distal tooth obsolete, then the elytral vestiture will be dense and conspicuously white and brown in color.....Group I, p. 40
- 3- With one femoral tooth (sometimes feeble); if femora also possess a minute distal tooth, the elytral intervals will be set with numerous erect setae, but the elytra will never have a dense vestiture of white and brown recumbent setae, and the protibiae will never be concave apically.....Group II, p. 94

#### GROUP I

The species of this group possess the following characteristics: two femoral teeth (proximal tooth in *tibialis* n. sp. and distal tooth in *nivosus* Lec. sometimes obsolete); first and second funicular segments of antennae

subequal in length and each longer than any of the succeeding segments; prothorax wider than long, with basal border bisinuate; elytral intervals 3, 5, 7, and 9 feebly to acutely costate; costa of interval 3 usually twice interrupted except in *falli* Blatch., *nivosus* Lec., and rarely *elegans* (Say); costa of interval 7 interrupted once or complete, that of interval 9 complete, extending from before base to near apex, where it is broader, less distinct, and united with costa of interval 3; interval 10 with a short basal elevation or costa; striae feebly impressed or lacking, more evident apically, succeeded by serial punctures, the latter usually more evident on basal half; vestiture usually condensed posteriorly to form a vague to prominent postmedian band; elytral intervals usually lacking suberect or erect setae; metasternum in males frequently grooved from meso- to metacoxa (Fig. 13); aedeagus with a dorsal plate (except in *nivosus* Lec.), this plate being separated apically from lateral plates by membranous areas (except in *seniculus* Lec.); transfer apparatus (except in *nivosus* Lec. and *seniculus* Lec.) with two roughly diamond-shaped plates (Fig. 4).

This group is commonly known as the "*nenuphar* group." The designation, however, appears to be a misnomer as only part of the group (species *juglandis* Lec. to *iowensis* n. sp.) is closely related to *nenuphar* (Hbst.). In addition, the remaining species fall into more or less closely related groups (*retentus-affinis*; *elegans-aratus*). Consequently, from a phylogenetic viewpoint it would appear desirable to consider the group only as Group I, omitting any designation of a "typical" species.

#### KEY TO SPECIES OF GROUP I

1. Abdominal sterna 3 and 4 with distinct, coarse punctures, density variable; elytral costa of interval 3 twice interrupted to form three, usually abrupt, elevations, of which the median one is usually hump-like and prominent..... 2
- 1- Abdominal sterna 3 and 4 with sparse, feebly impressed, fine punctures or with coarse punctures; if punctures are coarse the elytral costa of interval 3 (sometimes feeble) will be complete, once interrupted posteriorly, or twice interrupted and forming three feeble elevations, of which the median one is never hump-like and prominent; if specimens are less than 4 mm. and have a cream-colored postmedian elytral band and a depressed mesoscutellum, see Couplet 2; or if specimens have their elytral costae feeble and obscured by a dense, principally white and brown vestiture, see Couplet 10..... 6
2. Abdominal sternum 2 and usually sterna 3 and 4 sparsely punctate; mesoscutellum prominent; aedeagus with a feeble broad apical process (Figs. 42 and 69); size 5.9-7.1 mm..... *juglandis* Leconte, p. 44
- 2- Abdominal sterna 2 to 4 usually coarsely and densely punctate; if punctures are not dense, species will have a depressed mesoscutellum; size 3.2-6.0 mm..... 3
3. Mesoscutellum depressed, from lateral aspect gradually sloping downward basally (Fig. 29b)..... 4

- 3- Mesoscutellum prominent, from lateral aspect abruptly declivent basally (Fig. 30b)..... 5
4. Postmedian band of elytra consisting of reddish-brown or reddish-yellow and white recumbent setae; discal area between median elevations of costae of interval 3 intensely black and usually devoid of vestiture; males only with large dentate metaunci (Fig. 21); aedeagus with distinct apical process (Fig. 43).....*nenuphar* (Herbst), p. 48
- 4- Postmedian band of elytra consisting of all dirty white or cream setae, not mixed with reddish-brown or reddish-yellow setae; discal area between median elevations of costae of interval 3 with sparse to moderately dense vestiture; this area piceous but never intensely and prominently black; both sexes with non-dentate metaunci; aedeagus without an apical process. (Figs. 44 and 71).....*buchanani* new species, p. 51
5. Postmedian band of elytra composed of pure white setae and always extending laterally to costae of interval 7, usually to costae of interval 9; aedeagus as shown in Figs. 45 and 72.....*albicinctus* Leconte, p. 54
- 5- Postmedian band of elytra composed of reddish-yellow and white setae, the latter chiefly confined to the transverse discal area between the fifth intervals; aedeagus as shown in Figs. 46 and 73.....*iowensis* new species, p. 57
6. Abdominal sterna 1 to 4 with sparse, fine, feebly impressed punctures; sternum 1 frequently with coarser punctures along the base; sterna 3 and 4, in particular, smooth and with the feebly impressed punctures usually few in number..... 7
- 6- Abdominal sterna 1 to 4 with distinct coarse punctures, punctation usually dense, sometimes approaching moderate to sparse, but in such cases sterna 3 and 4 bear distinct, usually numerous, punctures..... 9
7. Postmedian elytral band obscure, composed of a mixture of brown and white setae (sometimes almost entirely of brown setae); setae of band usually not distinctly denser than those of area posterior to band; elytral costae of intervals 3 and 5 always twice interrupted; metaunci of male dentate or not dentate, those of female not dentate (Fig. 22); aedeagus with a narrow apical process (Fig. 47).....*retentus* (Say), p. 60
- 7- Postmedian elytral band usually distinct, between fifth intervals composed principally of white or light tannish setae or a mixture of the two, sometimes with a few brownish setae; band laterad of interval 5 sometimes less distinct and composed in part of brownish setae; setae of band distinctly denser than those of area posterior to band; elytral costa of interval 3 twice interrupted, that of interval 5 complete or interrupted once or twice; metaunci of male as in Figs. 23 and 24; aedeagus with a broad apical process (Fig. 48) or without a process (Fig. 49)..... 8
8. Male: metaunci feebly dentate or not dentate (Fig. 24); aedeagus with a broad apical process (Fig. 48); female: metaunci non-dentate; antennal scape distinctly not reaching head capsule (Fig. 36a), the distance between scape and head capsule at least one-half and usually two-thirds to three-fourths the length of first funicular segment of antenna.....*affinis* Boheman, p. 65
- 8- Male: metaunci distinctly dentate as shown in Fig. 23; aedeagus without an apical process (Fig. 49); female: metaunci non-dentate; antennal scape almost reaching head capsule (Fig. 36b), the distance between scape and head capsule less than one-half the length of first funicular segment of antenna.....*hicoloriae* new species, p. 69
9. Elytral costa of interval 3 evident and complete, rarely with a feeble interruption near apical declivity; prothoracic dorsum without a longitudinal

- oblique line of vestiture on each side; elytral vestiture sparse; aedeagus as shown in Figs. 50 and 77.....*falli* Blatchley, p. 72
- 9- Elytral costa of interval 3 nearly always twice interrupted, rarely without anterior interruption; when latter is lacking, prothoracic dorsum will have a longitudinal oblique line of vestiture on each side; sometimes, especially when elytral vestiture is dense and principally white and brown, the elevations formed by the interruptions are exceedingly feeble and obscure..... 10
10. Elytral costae feeble and obscured by dense, principally whitish vestiture; beak stout and shorter than non-carinate prothorax; aedeagus distinctly elongate, with an apical process but without a dorsal plate (Fig. 55).....*nivosus* Leconte, p. 73
- 10- Elytral costae usually distinct; elytral vestiture rarely dense; when dense, never in a large part white; beak usually longer than prothorax; when shorter, prothorax usually distinctly carinate; aedeagus, if elongate, without an apical process and with a distinct dorsal plate (Figs. 52 and 56)..... 11
11. Prothorax with a prominent longitudinal median carina and with two broad, deep depressions just behind the middle, one on either side of the carina; the oblique lines of vestiture on prothorax meeting in front; aedeagus elongate without an apical process and with an elongate dorsal plate (Fig. 56).....*seniculus* Leconte, p. 76
- 11- Prothorax feebly or not at all carinate; the oblique lines of vestiture on prothorax approaching but not meeting apically; aedeagus with or without an apical process but always with a broad dorsal plate (Figs. 52 and 53)..... 12
12. Male: both meso- and metaunci dentate (Fig. 25); aedeagus as shown in Figs. 51 and 78; female: all unci non-dentate; beak elongate, slightly curved (Fig. 39); the distance (a) between lateral apical emargination of beak and anterior margin of ball of antennal scape more than 1.5 times the distance (b) between dorsal and ventral surfaces of beak at position of antennal insertion (Fig. 105); first and second abdominal sterna densely punctate (Fig. 33); postmedian elytral band distinct in both sexes.....*elegans* (Say), p. 80
- 12- Male: metaunci dentate; mesounci not dentate; aedeagus as shown in Figs. 52, 53, or 54; female: all unci non-dentate; beak stout, curved (Fig. 41), the distance (a) being less than 1.5 times the distance (b); or beak slender (Fig. 40), in which case distance (a) is approximately 3 or more times distance (b) and the first and second abdominal sterna are moderately, never densely, punctate (density similar to that shown in Fig. 34); postmedian elytral band ill-defined and usually faint in both sexes..... 13
13. Beak elongate and slightly curved as shown in Figs. 37 and 40, never stout; fifth abdominal sternum at the most with two feeble tubercles; males without metasternal grooves between meso- and metacoxae and with the apical areas of the protibiae not compressed and not concave anteromedially; aedeagus elongate, without an apical process (Fig. 52).....*hayesi* new species, p. 85
- 13- Beak always stout and curved as shown in Figs. 38 and 41, sometimes shorter in male than shown in Fig. 38; fifth abdominal sternum usually with two distinct tubercles; males with or without metasternal grooves (Fig. 19); if grooves are absent, specimens will have apical portion of protibia compressed and concave anteromedially (Fig. 31a); aedeagus subrectangular with an apical process (Figs. 53 and 54)..... 14

14. Protibia of male normal (Fig. 31b); protibia of female with anterior surface at apical seventh not sloping medially, either convex or flattened; the oblique apical carina bearing the spinulae evident but not prominent; anterior aspect one-seventh before the apex not smooth, although the small ridges of the remainder of the tibia may be less distinct here, or shiny; usually with a distinct, though irregular, row of pale amber setae above the apical carina; aedeagus with apical process as in Fig. 53 ..... *aratus* (Germar), p. 88
- 14- Protibia of male compressed to form a median ridge on apical area of anterior surface, anteromedial apical surface distinctly concave (Fig. 31a); protibia of female with anterior surface at apical seventh sloping downward medially; the oblique apical carina bearing the row of prominent spinulae from lateral margin to uncus usually distinct, especially laterodorsally; anterior aspect, one-seventh before apex, usually smooth and shiny; pale amber setae in this area usually few and difficult to see; aedeagus with apical process as in Fig. 54 ..... *tibialis* new species, p. 91

*Conotrachelus juglandis* Leconte

*Conotrachelus juglandis* Leconte, 1876, Rhynchophora N. A., Proc. Amer. Philos. Soc., XV, No. 96, p. 226; Blatchley and Leng, 1916, Rhynchophora N. E. Amer., p. 468; Mutchler and Weiss, 1925, Conotr. N. J., Circ. 87, Bur. Stat. and Insp. Dept. Agr., N. J., p. 19.

*Length:* 5.9-7.1 mm.

*Special characters:* Elytra with a distinct, broad postmedian band, usually composed of whitish setae, sometimes a mixture of whitish and tannish setae; abdominal sternum 1 usually finely punctate.

*Color:* Prothorax, elytra, and abdomen reddish to black.

*Head:* Densely and evenly punctate; sparsely covered with brownish-yellow setae, posterior setae finer; beak curved for its entire length; longer than the prothorax, usually longer in female (2.00-2.37 mm.) than in male (1.75-2.05 mm.); in male dull, with three punctate, lateral sulci between base and antennal insertion, the median sulcus distinct apically but obscure basally, sometimes entirely obscure and replaced by punctures; dorsal surface broadly carinate from base to distad of middle, finely punctate; punctures dense distad of antennal insertion, coarser towards base and entering sulci; beak in female usually shining (sometimes dull), sulcate laterally, the lower sulcus distinct, the median and upper sulci being feeble and not extending more than halfway between base and antennal insertion; dorsal surface with a broad obscure carina basally, and with fine scattered punctures, the latter towards the base concentrated along the edges, coarser, and entering the sulci; sparse vestiture of brownish-yellow setae from base to distad of middle; in female setae chiefly in lowermost sulcus; antennae inserted approximately one-fourth from apex.

*Prothorax:* Sides widened for a short distance, narrowed up to one-third before apex, then suddenly constricted, sometimes smoothly rounded

from base to one-third before apex, instead of being angulate in outline on basal two-thirds; densely, coarsely, and unevenly punctate; disc with four tubercles (sometimes faint), one pair transversely at the middle, the other between median pair and base; a short carina extending from between median tubercles to apex, broad at base, narrowed toward apex; sparse vestiture of brownish-yellow and white elongate recumbent to subrecumbent setae; white setae on each side condensed into a sinuate, irregular line extending from basal angle to near apex; lines approach apically but do not meet; brownish-yellow setae more elongate than white ones.

*Mesoscutellum*: From lateral aspect, abruptly declivent basally.

*Elytra*: More than two-thirds as wide as long; sides subparallel for approximately one-half, then gradually converging to apex; basal border emarginate before humeri; humeri obliquely rounded and prominent; median elevation of interval 3 much more prominent than either of the other two and twice as long as posterior one; broad costa of interval 5 interrupted twice, elevations not as prominent as those of interval 3; costa of interval 7 narrower than those of intervals 3 and 5; serial punctures coarser on basal half, surface rough in appearance; sparse vestiture of brownish, brownish-yellow, and white elongate recumbent setae except posteriorly where whitish (dirty white or creamish) setae, sometimes mixed with tan ones, are condensed in a broad postmedian band; whitish setae also condensed at base of intervals 3 and 5; the line formed at base of interval 5 one-fourth the length of that at base of interval 3; remainder of vestiture mostly of brownish setae.

*Ventral surface*: Metasternum in male grooved from meso- to metacoxa (Fig. 19); groove absent in female. Abdomen shiny; sternum 1 finely punctured except for coarse punctures along anterior margin; coarse punctures sometimes in a single row, especially laterally, fine punctures rather dense medially but sparse laterally; sternum 2 sparsely and finely punctate; punctures of sterna 3 and 4 sparse to moderately dense and slightly coarser than those of sternum 2; sternum 5 more finely and densely punctate, punctures on basal border coarser, resembling those of preceding sternum, without tubercles; punctures each with a reddish-brown seta; lateral setae broader and light brownish-yellow and white in color, forming patches on sterna 2, 3, 4, and 5.

*Legs*: Metaunci of male dentate; those of female not dentate; legs with sparse vestiture of brownish-yellow and white setae; metafemora annulated with white setae, pro- and mesofemora feebly so.

*Male genitalia*: (Figs. 42 and 69). Aedeagus subelongate, nearly twice as long as wide and distinctly longer than the aedeagal struts, apex bisinuate to form a slight apical process; dorsal plate may or may not

extend under lateral plates, feebly prolonged to base; inner curvature at apex sometimes more angular than in Fig. 42. Length 1.03-1.06 mm., width at base .524-.572 mm., aedeagal struts .562-.687 mm.

*Type locality*: "Middle States."

*Lectotype*, hereby designated: Female, Museum of Comparative Zoology Type No. 5217-1, J. L. Leconte Collection (MCZ).

*Lectoparatype*: Female, M. C. Z. Type No. 5217-2, "Middle States," J. L. Leconte Collection (MCZ).

*Distribution*: "Ranges from Canada and New England west to Kansas, southwest to Texas and Louisiana, and south to Georgia," Britton and Kirk (1912). Records from: Canada (Montreal), Connecticut, District of Columbia, Illinois, Indiana, Iowa, Kansas, Kentucky, Maryland, Massachusetts, Michigan, Missouri, New Jersey, New York, North Carolina, Ohio, Pennsylvania, Virginia, West Virginia, Wisconsin.

*Biology*: The habits and biology of *C. juglandis* Lec. are better known than those of most species of *Conotrachelus*, Brooks (1922) and Britton and Kirk (1912) having made extensive studies on this curculio in West Virginia and Connecticut.

Commonly known as the butternut curculio, *juglandis* Lec. attacks various species of *Juglans*. Britton and Kirk (1912) list its hosts in order of preference as: *Juglans cordiformis* (heartnut), *J. sieboldiana* (Siebold's walnut), *J. cinerea* (butternut), *J. regia* (Persian or English walnut), *J. nigra* (black walnut), and *J. mandshurica* (Japanese walnut). The curculio attacks both the fruits and the stems of the first four hosts, but only the stems of the two last-named species. Brooks (1922) records *juglandis* Lec. doing serious damage to the fruits of *J. cinerea* and to the shoots and leaf petioles of *J. sieboldiana* and *J. cordiformis*. This worker also found adult curculios on the branches of *J. cathayensis*, and at the same time noted evidences of earlier larval injury to the branches.

The injury produced by the butternut curculio is brought about by the feeding of the adults in the nuts, tender tips, and leaf petioles, and by the burrowing of the larvae in the nuts, young shoots, leaf petioles, and stems. In the spring the adults make large punctures in the leaf, stems, and young shoots, sometimes causing them to wilt and die. Of more consequence, however, is the larval injury to the stems and branches. This type of injury is most serious on *J. sieboldiana* and *J. cordiformis*; *J. regia*, *J. cinerea*, and *J. nigra* being slightly or not at all attacked in this manner. In Connecticut small trees in nurseries and young transplanted trees have been severely and sometimes fatally damaged by larvae tunneling in the new growth. In some instances the new shoots were killed entirely back to the old wood. Brooks found similar serious injury to young trees in Massachusetts and New York.

Larval injury to the nuts is more extensive southward in Maryland and West Virginia where *J. cinerea* is most seriously attacked, *J. sieboldiana* and *J. cordiformis* showing only light infestations. Brooks (1922) states, "Many cases have been observed in which 50% or more of the nuts dropped from the trees prematurely on account of injury by the curculio larvae, the percentage of loss being greatest in years of light crops."

The butternut curculio passes the winter in the adult stage, probably in ground litter. In West Virginia the curculios appear at the time the walnut trees bloom and commence feeding upon the stems and leaf veins. After mating, the females begin oviposition, the first eggs being laid in the new growth, the later ones in the nuts. In *J. cinerea* the majority of the eggs are deposited in the nuts. At first the eggs are placed in crescent-shaped marks near the blossom end of the nuts, but later when the husks are tougher they are inserted in simple, gouged-out cavities in the side of the nut. The resultant larvae feed in the shoots and in the nuts, becoming full grown in 4 to 5 weeks, at which time they leave the host and enter the ground 1 to 3 inches for pupation. From one to six larvae develop in a nut, depending on its size. The curculio spends almost a month in the soil as a prepupa and pupa. On issuing from the ground in late summer and early autumn, the adults fly to the trees and feed on the leaf petioles and terminal shoots in a manner similar to that of the parent generation. With the oncoming of freezing weather the curculios go into hibernation.

Brooks (1922) lists six larval parasites of *juglandis* Lec.: *Chaetochlorops inquilina* Coq., *Cholomyia longipes* Fab., *Metadexia basalis* G.-T., *Cholomyia inaequipes* Bigot, *Myiophasia aenea* Wied., and *Sigalphus curculionis* Fitch. Of these six species Brooks reared the first two in abundant numbers.

In addition to the previously mentioned hosts, there are a few records in the literature of the occurrence of this species on hickory (Blatchley and Leng, 1916, and Britton and Kirk, 1912). Champlain and Knull (1921) question its occurrence on hickory, stating that it breeds in the leaf stems of walnut and butternut. Blatchley (1925), after collecting this species at Dunnedin, Florida, states (in reply to Champlain and Knull): "As the only species of Juglandaceae growing around Dunnedin belong to the genus *Hicoria* the weevil must breed in them if it is limited to that family for a host plant." From the available data its occurrence on hickory appears to be questionable.

Although Brooks (1922) states that he found no indication of *juglandis* Lec. breeding in *J. nigra*, Britton and Kirk (1912) record it as attacking that species. One specimen record substantiates the latter statement: "Reared from black walnuts" (Pa., Dr. Massey).

The butternut curculio has been collected "at lights" by H. S. Barber at Plummer's Island, Maryland.

*Remarks:* *C. juglandis* Lec. differs from all other species in the primary subdivision of Group I by its sparse and fine punctation of the second, and usually the third and fourth, abdominal sterna. The dentate metaunci of the male indicates an affinity with *nenuphar* (Hbst.), but by genital characteristics *juglandis* Lec. and *buchanani* n. sp. seem more closely linked. The occurrence of this type of divergent affinity is prevalent in this primary division of Group I, and consequently definite phylogenetic placements of the species cannot be made.

That Leconte (1876) had only female specimens before him when he described *juglandis* is indicated by his description of the beak as being sparsely punctate and bearing a broad, lateral groove and two short, finer, basal ones. Examination of Leconte's cotypes verifies this viewpoint. Blatchley's description in 1916 similarly indicates his examination of only female specimens.

This insect was first recognized as possibly distinct from *C. nenuphar* (Hbst.) by B. D. Walsh (1868), who sent specimens to Leconte, but the latter diagnosed them merely as large varieties of *nenuphar* (Hbst.). Walsh, however, never found this new form in stone fruits nor *nenuphar* (Hbst.) in walnuts and, therefore, still considered the two as distinct species, calling the walnut-infesting curculio a "phytophagic species." He did not, however, describe his phytophagic species. Leconte (1876) recognized the walnut-infesting form as distinct from *nenuphar* (Hbst.) and described it as *juglandis*.

#### *Conotrachelus nenuphar* (Herbst)

*Curculio nenuphar* Herbst, 1797, Kafer, Natursystem aller Insekten, VII, p. 29.

*Conotrachelus nenuphar* (Hbst.) Leconte and Horn, 1876, Rhynchophora N. A., Proc. Amer. Philos. Soc., XV, No. 96, p. 227; Provancher, 1877, Faune Ent. Can. I Col. p. 529; Blatchley and Leng, 1916, Rhynchophora N. E. Amer., p. 469.

*Rhynchaenus argula* Fabricius, 1801, Syst. Eleut. II, p. 467.

*Cryptorhynchus argula* (Fab.) Say, 1831, Desc. N. A. Curc. New Harmony, Indiana, p. 19, in Writings of Thomas Say, ed. Leconte, 1859, p. 285; Fahreus, 1837, Schönh. Gen. Spec. Curc., IV, pt. 1, p. 425.

*Rhynchaenus cerasi* Peck, 1819, Mass. Agric. Repos. and Journ., V, p. 312.

*Length:* 3.6-5.4 mm.

*Special characters:* Abdominal punctation of sterna 1 and 2 exceedingly dense; numerous punctures frequently more oblong than circular in outline; postmedian elytral band usually not prominent, the white setae confined mesad of interval 4.

*Color:* Prothorax and elytra red and black mixed, proportion of each varying greatly in different specimens.

*Head:* Semi-coarsely punctate; with sparse vestiture of reddish-brown and white setae; basal setae finer; beak strongly curved (Fig. 35); curvature more abrupt apically in male; beak approximately as long as prothorax, equal in length in both sexes; three lateral sulci between base and antennal insertion; the median sulcus sometimes faint or replaced by large, shallow punctures; dorsal surface with a feeble, broadly rounded carina from base to distad of middle, usually more evident in male; area distad of carina with sparse to dense elongate punctures, those of female sometimes fine; sparse vestiture of reddish-brown and white setae proximad of antennal insertion, setae arising from sulci; antennae inserted approximately one-fourth to one-third before apex of beak, insertion in females usually nearer one-third, that of males usually nearer one-fourth.

*Prothorax:* Sides feebly rounded or subparallel, with an apical constriction; densely, coarsely, and roughly punctate; four tubercles on disc, one pair transversely at the middle, the other between median pair and base; median pair prominent, much more so than posterior pair which is sometimes evanescent; area between median and posterior tubercle on each side sometimes depressed; disc carinate longitudinally from between median tubercles to apex; carina varying from distinct to feeble, sometimes extending to posterior tubercles; sparse vestiture of reddish-brown to yellow and white, elongate, recumbent to subrecumbent setae; white setae on each side condensed into a sinuate line from inside the basal angle to before apex; lines approach but do not meet apically; apical portion of white lines sometimes lacking, so that remaining basal portions appear as two short, distinct bars; remainder of vestiture chiefly reddish-brown with a few patches of white; white markings of the vestiture not always prominent in dried specimens.

*Elytra:* Approximately two-thirds as wide as long; sides subparallel for more than half, then gradually converging to apex; humeri obliquely rounded, prominent; basal border emarginate before humeri; the median elevation of interval 3 distinctly more prominent than others; costa of interval 5 twice interrupted, with median elevation most prominent but less so than median one of interval 3, posterior elevation longer than either anterior or median elevations; interval 7 usually with costa more acute than those of intervals 3 and 5; serial punctures large on basal half but not always distinctly impressed; sparse vestiture of brown, reddish-brown, reddish-yellow, and white recumbent setae, the reddish-yellow and white setae forming a postmedian band in which white setae are chiefly confined to the transverse discal area between the third intervals, the patch at base of posterior elevation of interval 3 sometimes extending over into interval 4; postmedian band usually not prominent

(white setae rarely absent in band); white setae also condensed in a line at base of intervals 3 and 5.

*Ventral surface:* Metasternum in male grooved from posterior margin of mesocoxa to anterior margin of metacoxa (Fig. 19); groove absent in female. Abdominal sterna with even, coarse, and extremely dense punctation; punctures with scarcely any space between them, especially on sternum 2, and tending to be confluent in many areas; sternum 5 with punctures smaller than those of preceding sterna and with lateral depressions, but occasionally depressed medially, with feeble to prominent tubercles; each puncture with a fine reddish-brown seta, except laterally and on the basal border of sternum 5, where setae are broader and reddish-yellow; lateral setae forming patches on sterna 2 to 5.

*Legs:* Proximal femoral tooth larger; in male metaunci broad and dentate (Fig. 21), in female narrow and non-dentate; all tibiae in female minutely but distinctly mucronate proximad of uncus; legs sparsely clothed with elongate reddish-brown, reddish-yellow, and white setae; metafemora with a dense patch of reddish-yellow to yellow setae at position of teeth.

*Male genitalia:* (Figs. 43 and 70). Aedeagus approximately one-third longer than wide, and approximately one-third longer than aedeagal struts; apex of aedeagus with a narrow process, lateral emargination of outer curvature variable in distinctness, sometimes lacking; dorsal plate may be wider than in Fig. 43. Length .596-.673 mm., width at base .387-.423 mm., aedeagal struts .349-.423 mm.

*Type locality:* North America.

*Type:* Probably in Zool. Mus. Berlin.

*Distribution:* "Ranges from Nova Scotia to Manitoba and Colorado, south to Largo, Florida, and the eastern half of Texas," Chapman (1938). There is also a record by Cooley (1922) of its occurrence in Bitter Root Valley, Montana, and the writer has one specimen labelled "Mon." *C. nenuphar* (Hbst.) is the most abundant species in the genus, and no individual locality records were kept for it.

*Biology:* Since this species is of much economic importance, there is available a mass of literature pertaining to its life history, food plants, distribution, natural enemies, and control. The reader is referred to Chapman (1938), Snapp (1930), and Quaintance and Jenne (1912) for details of the biology of *C. nenuphar* (Hbst.). It appears desirable, however, to mention that the following types of fruits have served as hosts: plum, cherry, peach, nectarine, apple, wild crabapple, pear, and quince. It has also been reported by Quaintance and Jenne (1912) as occasionally ovipositing in the fruits of huckleberry, grape, strawberry, currant, gooseberry, and persimmon. In addition, Chapman (1938) states that it has

been found breeding in the callous tissue formed on plums affected with black knot disease. This report agrees with the following data found on a specimen from Bar Harbor, Maine: "Bred August 27, 1935, black knot cherry, reared, breeding in fleshy part of fungus, 2 more ex. (♀) in Coll. W. E. Brower."

*Remarks:* This species is closely allied to *juglandis* Lec., *buchanani* n. sp., *iowensis* n. sp., and *albicinctus* Lec. The narrow apical process of the aedeagus in *nenuphar* (Hbst.) is a character not found in these four species and serves to indicate that on the basis of the male genitalia *nenuphar* (Hbst.) is not as closely related to these species as they are to each other. The characters in the key will readily separate *nenuphar* (Hbst.) from its allied species.

*Conotrachelus buchanani* n. sp.

*Length:* 3.1-5.4 mm.

*Special characters:* Postmedian band of elytra prominent and extending laterad of interval 5; abdominal sternum 1 usually so densely rugulose that coarse punctures in median area are less evident than those of succeeding sterna.

*Color:* Prothorax and elytra piceous, black, and reddish-brown mixed.

*Head:* Semi-coarsely and densely punctate; clothed with white and brownish-yellow elongate setae, sometimes so densely as to obscure punctures; beak distinctly curved for its entire length; longer than prothorax, equal in length in both sexes; trisulcate laterally between base and antennal insertion; upper and lower sulci distinct; median sulcus usually obscure basally; lower sulcus occasionally dividing basally; sulci punctate; dorsal aspect broadly and feebly carinate from base to distad of middle; area distad of carina with elongate, fine punctures, variable in density; surface sometimes smooth medially; sparse vestiture of whitish and brownish-yellow elongate setae on basal two-thirds; antennae inserted one-fourth to one-third from apex.

*Prothorax:* Sides usually subparallel and constricted subapically, occasionally slightly rounded; coarsely, densely, and unevenly punctate; disc with four tubercles, one pair transversely at middle, the other between median pair and base; median pair more prominent; a short, median, longitudinal carina (frequently feeble and vague) from between anterior tubercles to before apex; sparse to moderately dense vestiture of brown, brownish-yellow, and white elongate recumbent to subrecumbent setae; whitish and light-yellowish setae on each side, forming a sinuate line from basal angle to near apex, each line also sending a branch medially, the branches from each side uniting between the median pair

of tubercles; lines sometimes obscure (especially in specimens 3-4 mm.) or broken up into separate sections; brownish and yellowish setae usually more elongate than white ones.

*Elytra*: More than two-thirds as wide as long; sides subparallel for approximately one-half, then gradually converging to the apex; humeri obliquely rounded and prominent; basal border emarginate mesad of humeri; elevations of interval 3 varying in prominence, the median elevation being twice as long as the posterior one and the most prominent; broad costa of interval 5 twice interrupted, with median elevation sometimes not distinctly separated from anterior one; anterior, especially, and occasionally median, elevation feeble; costa of interval 7 narrower and less prominent than preceding ones, interrupted once behind the base; serial punctation coarse, most evident basally; moderate to dense vestiture (sometimes rather sparse but specimens appear rubbed) of brown, brownish-yellow, and dirty white elongate recumbent setae; the whitish, usually cream, setae condensed in a broad postmedian band and in a longitudinal line at base of intervals 3 and 5; the line of vestiture of interval 3 twice the length of that of interval 5; remainder of vestiture mostly of brown and brownish-yellow setae with scattered patches of white.

*Ventral surface*: Metasternum in male feebly grooved from meso- to metacoxa; groove absent in female. Abdomen with sterna 1 to 5 moderately to densely punctate (in specimens 3-4 mm. punctation of sterna 2, 3, and 4 sometimes approaching sparse); sterna 2 to 4 and occasionally 5 sometimes less densely punctate than sternum 1, the latter usually more coarsely punctate than the succeeding sterna; sternum 5 with two feeble to distinct tubercles; each puncture with a fine reddish-brown or amber seta; lateral setae broader and white or yellow in color, forming small patches on sterna 2 to 5; broader setae of fifth sternum more closely approaching the median line.

*Legs*: Proximal femoral tooth usually broader at base than distal one; female with a small mucro proximad of uncus, most evident on protibiae; male without mucrones; legs sparsely covered with brownish-yellow and whitish setae; metafemora usually distinctly annulated with dirty white and yellow elongate setae; pro- and mesofemora faintly ringed.

*Male genitalia*: (Figs. 44 and 71). Aedeagus subrectangular dorsally, one-fourth to one-third longer than wide at the base and one-fourth to one-half longer than the aedeagal struts; apex bisinuate and with a feeble process; laterally, ventral curvature smooth from base to apex. Length .386-.687 mm., width at base .250-.471 mm., aedeagal struts .250-.500 mm.

This species is named for Mr. L. L. Buchanan of the United States National Museum.

*Type locality:* New Braunfels, Texas.

*Holotype:* Male, June 27, 1895, H. Soltau, United States National Museum Type No. 54307 (USNM).

*Allotype:* Female, San Antonio, Texas, June 24, 1895, H. Soltau (USNM).

*Paratypes:* DISTRICT OF COLUMBIA, ♂, (USNM); ILLINOIS: Urbana, Univ. of Ill. Woods, Sept. 11, 1937, Shrubs, ♂, (HFS); IOWA: Lake Okoboji, July 1, 1916, L. L. Buchanan, ♀, (USNM); KANSAS: Topeka, Ac. No. 976, Popenoe, ♂, (USNM); Onaga, July 8 and 21, Wickham, 1 ♂, (WPH), 2 ♂, (USNM); Kansas, T. B. A., ♀, (WPH); Riley Co., June, Marlatt, ♀, (WPH); MARYLAND: Plum Point, May 28, 1922, L. L. Buchanan, ♂, (HFS); NEW JERSEY: Riverton, Sept. 11, 1898, Geo. M. Greene Collection, ♂, (USNM); TEXAS: New Braunfels, June 27, 1895, H. Soltau, 4 ♂, 1 ♀, (USNM); Dallas, July, 1907, W. W. Yothers, ♂, (USNM); Dallas, March 15, 1908, and March 18, 1909, F. C. Bishopp, 3 ♂, (USNM), 1 ♀, (HFS); San Antonio, June 24, 1895, H. Soltau, 1 ♂, 2 ♀, (USNM); Kerrville, April 27, 1908, on pecan, F. C. Pratt, ♂, (USNM); Columbus, June 2, H. Soltau, 2 ♀, (USNM); Brownsville, May 13 and 29, 1904, H. Soltau, 2 ♀, (USNM).

*Distribution:* Ranges from New Jersey and Pennsylvania south to Louisiana, southwest to Texas, and west to Utah. Common in eastern Texas. Locality records from specimens not in type series: District of Columbia, Illinois (Galesburg), Louisiana (New Iberia), Maryland (Plummer's Island), Missouri (Sedalia, Kansas City), Ohio (Cincinnati), Pennsylvania, Texas (Austin, Alpine, Victoria), Utah, and Virginia (Acquia, Middletown, Nelson County, Fairfax County).

*Biology:* Two specimen records here cited indicate that *buchanani* n. sp. is associated with hackberry: "Celtis" (Plummer's Island, Md., A. D. Hopkins) and "on *Celtis mississippi*" (Victoria, Texas, J. D. Mitchell). Since this species and *albicinctus* Lec. heretofore have been considered as one species, the few literature records listed under *albicinctus* Lec. (p. 56) are also applicable to *buchanani* n. sp.

*Remarks:* This species is closely allied to *albicinctus* Lec. and has previously been identified as that species. It is distinguished from *albicinctus* Lec. by the shape and slope of the mesoscutellum, as stated in the key. Usually *buchanani* n. sp. also has a denser vestiture of the prothorax and of the elytra, especially on interval 3 anterior to the median elevation. Males of these two species are easily separated by their genitalia. From a study of Leconte's specimens it is evident that he considered both *buchanani* n. sp. and *albicinctus* Lec. as *albicinctus* Lec., and a discussion of which species is *albicinctus* Lec. appears under that species (p. 56).

The great range in size variation in this species, from 3.1 to 5.4 millimeters, at first was thought to indicate a size variety, since the specimens on hand could be distinctly divided into two groups, one above 4.1 millimeters and the other below 3.8. When other specimens became available, however, this distinction disappeared and consequently no varieties have been erected. Specimens at the extremes of length seem distinct, but in a long series one series can be shown to merge into the other.

*Conotrachelus albicinctus* Leconte

*Conotrachelus albicinctus* Leconte, 1876, Rhynchophora N. A., Proc. Amer. Philos. Soc., XV, No. 96, p. 226; Blatchley and Leng, 1916, Rhynchophora N. E. Amer. p. 469.

*Length:* 3.9-4.8 mm.

*Special characters:* Postmedian elytral band broad longitudinally and prominent, composed of white setae; sometimes in areas where white setae have been rubbed off a few yellowish setae are visible; when vestiture of band is complete, however, it is pure white in appearance.

*Color:* Prothorax and elytra piceous to black.

*Head:* Coarsely and densely punctate; sparsely covered with brownish-yellow, yellow and white elongate setae; basal setae finer; beak curved from base to apex; longer than prothorax, equal in length in both sexes; three lateral sulci between base and antennal insertion; median sulcus obscure toward the base; sulci varying in depth in different specimens, sometimes being very feeble, especially toward the base; sulci punctate; dorsal surface broadly carinate from base to over half its length; area distad of carina in male with fine elongate punctures; in female shining, more finely and less densely punctate; sparse covering of brownish-yellow and white setae from base to distad of middle; antennae inserted approximately two-sevenths from apex of beak.

*Prothorax:* Sides subparallel, then constricted apically; sometimes rounded from base to apical constriction; coarsely, densely, and unevenly punctate; with four tubercles, one pair transversely at middle, the other between median pair and base, with median pair most prominent; a feeble longitudinal carina from between median tubercles to apex (sometimes absent); sparse vestiture of white and light brownish-yellow recumbent to subrecumbent setae; the latter colored setae more elongate than the former; the white setae on each side condensed into a sinuate line which in some specimens extends from the basal angle to near the apex, the lines gradually converging apically, majority of setae longer than those of elytra.

*Elytra:* Approximately one-fourth to one-third longer than wide; sides subparallel for approximately two-thirds, then gradually converging

to the apex; humeri obliquely rounded and prominent; basal border mesad of humeri emarginate; median elevation of interval 3 twice as long as posterior elevation and more prominent than either of the other two; broad costa of interval 5 interrupted twice, with the median elevation smaller and less prominent than the median one of interval 3; costa of interval 7 narrower than costae of intervals 3 and 5; serial punctures coarse and dense, closer together apically, giving surface a roughened appearance; vestiture of brownish-yellow and pure white, elongate, recumbent setae which are extremely sparse on the disc between and anterior to the median elevations of the third intervals; white setae condensed, in addition to the postmedian band, in a brief line at base of intervals 3 and 5, that of the latter being approximately half as long as that of the third; remainder of vestiture sparse, mostly of brownish-yellow setae.

*Ventral surface:* Metasternum in male grooved from meso- to metacoxae; groove absent in female. Abdominal sterna coarsely and densely punctate; punctures of sternum 2 sometimes smaller than those of 1; sternum 5 more finely and densely punctate than others, without tubercles; each puncture with a light reddish seta; setae along lateral margins broader, and white to reddish-brown in color; lateral setae in some specimens forming easily observed patches.

*Legs:* Proximal femoral tooth larger at base than prominent distal one; metaunci in both sexes non-dentate; legs with sparse covering (except for annulation) of brownish-yellow and whitish setae; metafemora distinctly annulated with pure white setae.

*Male genitalia:* (Figs. 45 and 72). Aedeagus not subrectangular, approximately twice as long as wide at base, distinctly longer than aedeagal struts; dorsal plate extending to base, neck of plate sometimes wider than in Fig. 45; apex of aedeagus bisinuate and forming a feeble process; ventral curvature angled approximately one-fourth from apex. Length .673-.687 mm., width at base .324-.363 mm., aedeagal struts .363-.406 mm.

*Type locality:* Texas.

*Lectotype*, hereby designated: Male, Museum of Comparative Zoology Type No. 5214-3, J. L. Leconte Collection (MCZ).

*Lectoparatype:* Female, M. C. Z. Type No. 5214-2, Southern States, J. L. Leconte Collection (MCZ).

*Distribution:* "Ranges from Michigan and District of Columbia to Georgia, Florida, and Texas," Blatchley and Leng (1916). The locality data from which the above range was calculated may in part refer to *buchanani* n. sp., but the records below indicate that this range is appli-

cable to *albicinctus* Lec. Above range extended north to Massachusetts, and west to Iowa and Kansas. Records from: Illinois, Iowa, Kansas, Massachusetts, Southern States (Georgia?), South Carolina, and Texas.

*Biology:* Pierce (1907a) reports a number of *albicinctus* Lec. beaten from *Clematis drummondii* and *Celtis* in a palmetto jungle at Santo Tomas, Texas. The same writer (1916) reports breeding this species from a gall on *Cornus candidissima* Marsh. The only available specimen record reveals its occurrence "on *Cornus*" at Dallas, Texas. As mentioned on page 53, however, the literature records given here may apply equally well to *buchanani* n. sp. When the specimen records for both species are considered in relation to the literature records, however, it appears probable that Pierce's first record has reference to *buchanani* n. sp. and his second to *albicinctus* Lec.

*Remarks:* *C. albicinctus* Lec. is closely related to both *buchanani* n. sp. and *iowensis* n. sp., and it is difficult to state to which of these *albicinctus* Lec. has the greatest affinity. By its elytral band *albicinctus* Lec. bears a closer resemblance to *buchanani* n. sp., but by the possession of a prominent mesoscutellum it is nearer to *iowensis* n. sp.

*C. albicinctus* Lec. has been confused with *nenuphar* (Hbst.) and has formerly had included with it all the specimens now designated as *buchanani* n. sp. The misidentification of *nenuphar* (Hbst.) as *albicinctus* Lec. has probably been due largely to superficial examination of the specimens. Both *buchanani* n. sp. and *albicinctus* Lec., however, have been grouped together as *albicinctus* Lec. by coleopterous workers. In the Leconte collection at the Museum of Comparative Zoology there are three cotypes of *albicinctus*, of which the first one in the series is *buchanani* n. sp. and the other two *albicinctus* Lec. Ordinarily the first specimen in a series of cotypes would be considered the type, and by this procedure the species now designated *buchanani* n. sp. would have taken the name *albicinctus* Lec. The first cotype, however, bears the locality label "Utah," and Leconte's original description states the distribution as "Southern States, Georgia to Texas," so that this specimen no doubt was received by him after the original description was published, and therefore cannot be considered as a type representative of the species described by Leconte (1876) as *albicinctus*. The second specimen is from "Southern States" and the third from Texas, so that the writer is quite certain that these are the specimens on which the original description of *albicinctus* Lec. was based. Consequently, the third specimen labelled *albicinctus* in the Leconte Collection, a male, 4.8 mm., MCZ Type No. 5214-3, is hereby designated the lectotype of *albicinctus* Leconte. The third specimen was selected instead of the second because of its definite locality.

*Conotrachelus iowensis* n. sp.

*Length:* 4.10–4.65 mm.

*Special characters:* Prothorax and elytra dark reddish and black; black on elytra chiefly confined to two prominent transverse bands, one medially, extending laterally to the median elevation of interval 5 on each side, the other on the apical declivity posterior to the apical elevations of intervals 3 and 5; prominence of color bands principally due to lack of vestiture in these areas.

*Head:* With dense semi-coarse punctures and with a moderately dense covering of mainly reddish-yellow setae but also with a few white ones, the latter chiefly between the eyes; vestiture sometimes rubbed off to a large degree; beak stout, with curvature slightly greater than that shown in Fig. 35; shorter than or equal to prothorax in length, equal in length in both sexes; trisulcate laterally between base and antennal insertion; upper and median sulci feeble and indistinct, the median one sometimes absent partway or replaced entirely by large punctures; upper sulcus sometimes distinct in male; lower sulcus distinct; male sometimes, when upper sulcus is distinct, with a faint broadly rounded carina on dorsal surface from base to distad of middle; dorsal aspect below antennal insertion with sparse to moderately dense elongate punctures; punctures denser along the sides and extending basally in two lateral series; sparse vestiture of reddish-yellow setae arising from sulci or from punctures replacing sulci, with a few white setae also present; antennae inserted approximately one-fourth to one-third from apex.

*Prothorax:* Sides feebly rounded or subparallel to approximately one-sixth before apex, then constricted; densely and coarsely punctate; punctures less evident along apical border; with six tubercles, one pair transversely at the middle, a second between the median pair and the base, and the third consisting of two widely separated tubercles, each located on the lateral slope behind the middle, the tubercles on each side of midline forming a triangle; median pair of tubercles always evident, but other pairs sometimes obsolete or sometimes with one tubercle of the pair feeble and obscure; tubercles rounded or flat on top; disc non-carinate or with a feeble longitudinal carina extending apically from between or posterior to median tubercles; sparse vestiture of reddish-yellow and white recumbent to subrecumbent setae; white setae on each side condensed in a sinuate line from inside of basal angle to before apex; lines approach apically but do not meet; the sinuate lines with short side branches, a median one between the median and posterior pairs of tubercles, and an oblique lateral branch apically; the majority of reddish-yellow setae approximately twice the length of white ones; some speci-

mens with vestiture, in part, rubbed off so above characteristics are not evident.

*Elytra*: Approximately three-fourths as wide as long; sides subparallel for approximately half, then gradually converging to the apex; humeri prominent and obliquely rounded; basal border emarginate before humeri; median elevation of interval 3 the longest and most prominent; interval 5 with a broad costa similarly interrupted as that of interval 3, but with elevations respectively less prominent, especially the median and posterior ones; posterior elevation of interval 5 as long as or longer than median one of interval 3; costa of interval 7 acute and complete except in one female where, on one side, it becomes so feeble laterad of the median elevation of interval 5 that it appears interrupted; serial punctures large and distinct on basal half but becoming smaller and less distinct apically; sparse vestiture of reddish-yellow and white recumbent setae; vestiture dense in a postmedian band in which white setae are chiefly condensed anteriorly in the area between intervals 3 and 5 (i.e., adjacent to and laterad of posterior half of median elevation of interval 3) with the reddish-yellow setae behind them; sometimes a few reddish-yellow setae intermixed with the anterior white ones; portion of band mesad of interval 3 with a mixture of reddish-yellow and white setae, or with white setae forming a narrow transverse band; white setae also condensed in a brief line at base of intervals 3 and 5; remainder of vestiture mostly reddish-yellow setae with scattered small patches of white ones; setae few in number or absent in area posterior to apical elevations of intervals 3 and 5 and in transverse area between median elevations of interval 5.

*Ventral surface*: Metasternum not grooved from meso- to metacoxa in either sex. Abdominal sterna 1 to 4 coarsely and densely punctate; punctures, especially of sterna 1 and 2, distinct and round, with the majority large; sterna 3 and 4 usually with punctures smaller than the majority of those of sterna 1 and 2; sternum 4 sometimes with finer punctation than 3; sternum 5 with punctures smaller than those of preceding sterna; punctures finer apically, usually without tubercles, but sometimes with a faint indication of a pair on the apical third; each puncture with a pale, amber seta; setae broader along the sides, usually white but sometimes reddish-yellow; sometimes faint lateral patches of vestiture on sterna 3 and 4.

*Legs*: Femoral teeth small but distinct, either equal in size or with proximal tooth largest; metaunci in both sexes non-dentate; femora and tibiae with sparse vestiture of reddish-yellow and white setae, except on apical half of metafemora, where vestiture is dense; abundance of white setae, increasing from profemora to mesofemora to metafemora, forming

on the latter a broad band at position of femoral teeth and a narrow band subapically.

*Male genitalia:* (Figs. 46 and 73). Aedeagus more than half as wide at base as long, and approximately twice as long as aedeagal struts; outer curvature near apex widened; apex faintly bisinuate and with a feeble process; dorsal plate sometimes extending nearer base than in Fig. 46. Length .562-.625 mm., width at base .324-.349 mm., aedeagal struts .262-.349 mm.

*Type locality:* Iowa City, Iowa.

*Holotype:* Male, United States National Museum Type No. 54308, May 17, 1917, L. L. Buchanan.

*Allotype:* Female, White Heath, Illinois, April 30, 1916 (ISNHS).

*Paratypes:* IOWA: Iowa City, May 17, 1917, L. L. Buchanan, ♀, (WPH); Clayton County, June 15, 1932, Barker, ♀, (HFS); Hardin County, June 20, 1934, H. C. Knutson, ♂, (HFS); Dickinson County, June 18, 1936, ♂, (IISC); Mt. Pleasant, April 14, 1930, H. Essex, ♂, (USNM).

*Distribution:* Range restricted to Iowa and Illinois.

*Biology:* No biological data are available for this species.

*Remarks:* This species is a close relative of *albicinctus* Lec., *buchanani* n. sp., and *nenuphar* (Hbst.). It has been confused with *nenuphar* (Hbst.) and labeled as such, but the two can easily be distinguished by the characters in the key. The exact relationship between these four species is difficult to determine, as the evaluation depends on the criterion used. If only the male genitalia are considered, *nenuphar* (Hbst.) appears isolated from the other three species; if the mesoscutellum is used as a criterion, *nenuphar* (Hbst.) and *buchanani* n. sp. fall in one group, and *albicinctus* Lec. and *iowensis* n. sp. in the other; and if their relationships are measured by the coloration of the postmedian band, *iowensis* n. sp. is linked to *nenuphar* (Hbst.), and *buchanani* n. sp. and *albicinctus* Lec. stand together. It appears that all four species recently arose from a common line of descent, but their relationships beyond that point are not clear.

Although this species has been found only in Iowa and Illinois, it may exist in some of the other states included in this study, since specimens of *nenuphar* (Hbst.) usually were not included in loans, and *iowensis* n. sp. has been misidentified as the plum curculio. However, in one hundred and forty specimens of *nenuphar* (Hbst.) in the Illinois State Natural History Survey collection, thirty-five from Massachusetts State College, thirty from the Bureau of Entomology and Plant Quarantine, Fort Valley, Georgia, an estimated five hundred from the Museum of

Comparative Zoology and United States National Museum, and specimens from Pennsylvania, New Hampshire, Montana, Florida, Kansas, and North Carolina, only two *iowensis* n. sp. have been found. This would seem to indicate that the species is not common.

In the United States National Museum collections, two small male specimens (3.0 and 3.45 mm.) resembling *iowensis* n. sp. were obtained. These specimens from Michigan and Ontario differ from *iowensis* n. sp. primarily in that the postmedian band lacks the prominent patch of white setae in the area between intervals 3 and 5 and that the beak is distinctly carinate and trisulcate. The aedeagi of these forms are similar to that of *iowensis* n. sp., excepting that the dorsal plate extends distinctly to the base and the inner curvatures (except apically) are parallel. Otherwise these specimens are the same as *iowensis* n. sp. They possibly are *iowensis* n. sp. or its closest relative. Tentatively, until further material is available, the two specimens have been referred to *iowensis* n. sp., although excluded from the type series.

*Conotrachelus retentus* (Say)

*Cryptorhynchus retentus* Say, 1831, Desc. N. A. Curc. New Harmony, Indiana, p. 27, in Writings of Thomas Say, ed. Leconte, 1859, p. 295.

*Conotrachelus retentus* (Say) Boheman, 1837, Schönh. Gen. Spec. Curc., IV, pt. 1, p. 442; Leconte and Horn, 1876, Rhynchophora N. A., Proc. Amer. Philos. Soc., XV, No. 96, p. 227; Blatchley and Leng, 1916, Rhynchophora N. E. Amer., p. 470.

*Length:* 5.70-7.25 mm.

*Special characters:* Prothorax and elytra brown to reddish; elytra with sparse to moderately dense vestiture of recumbent setae which are chiefly tan to brownish but sometimes white; numerous setae only about half the length of those on femora; specimens under low power with brownish or grayish cast; posterior elevation of interval 5 longer than median elevation of intervals 3 and 5; costal elevations presenting a somewhat even appearance.

*Head:* Coarsely, distinctly, and densely punctate; with a few scattered white and light tannish elongate setae, or with a sparse vestiture of similar colored setae; beak curved, longer than prothorax; beak slightly longer in female (2.2-2.4 mm.) than in male (1.6-1.9 mm.); male with beak more sharply curved apically and with three lateral sulci between base and antennal insertion; median sulcus frequently obscure, with area occupied by large punctures; lower sulcus broad, sometimes being divided into two sulci, with large punctures; dorsal surface usually with a broad rounded carina from base to distad of middle; the tip distad of antennal insertion with dense elongate punctures; female beak with three lateral punctate sulci between base and antennal insertion; median and

lower sulcus being distinct and reaching from base to distad of middle; upper sulcus faint, marked by rows of fine punctures, much shorter than other sulci, and usually not extending distad of middle; dorsal aspect not carinate; tip with fine sparse punctures distad of antennal insertion; punctures condensed laterally and basally in two lines, so that median portion is smooth proximad of the antennal insertion; both sexes with sparse vestiture of light tan and whitish setae proximad of antennal insertion; setae sometimes absent except for a few basally; antennae inserted at approximate apical third in female, and at apical fourth to fifth in male.

*Prothorax*: Apical constriction either abrupt or gradual; sides usually smoothly rounded from base to apical third, the outline sometimes presenting an even curve from base to apex, but occasionally being obtusely angulate on the basal two-thirds; outline sometimes varying on opposite sides; densely punctate, punctures shallow, usually distinct, and most evident laterally; disc with four indistinct tubercles (sometimes absent), with one pair transversely at the middle and the other between the median pair and the base; disc sometimes depressed between median and posterior tubercles on each side, the depressions accentuating the tubercles; a small, median callus (sometimes obscure) between median tubercles, with callus sometimes extending narrowly forward as a short carina or entirely replaced by a short median carina; sparse vestiture of white and tan recumbent to subrecumbent setae; setae sometimes absent on disc; whitish setae on each side condensed into a sinuate line extending from near basal angle to apex; lines approaching each other apically, in some specimens obscure and almost obliterated; tan setae more elongate than white ones.

*Mesoscutellum*: From dorsal aspect apex usually broadly rounded; from lateral aspect sloping basally, with slope occasionally steep or even abrupt.

*Elytra*: Approximately two-thirds as wide as long; sides subparallel for about one-half, then gradually converging to apex; humeri obliquely rounded and prominent; basal border emarginate before humeri; intervals 3, 5, 7, and 9 moderately and evenly costate; elevations of interval 3 distinct although not prominent; elevations sometimes subequal in length, or the median one longer than either of the other two; anterior elevation less evident than posterior and median ones; costa of interval 5 interrupted twice, but with posterior elevation always longest and subequal in prominence to median one; costa of interval 7 finer than those of intervals 3 and 5; serial punctures large and exceptionally distinct in some specimens; elytra with sparse to moderately dense vestiture of brownish-tan and white recumbent setae; majority of setae tan to brown; white setae mainly arising from punctures and condensed in small patches

on basal border between costae of intervals 3 and 5; sometimes also condensed between median and posterior elevations of interval 3; these latter white setae together with the lighter brownish-tan setae form the vague postmedian band.

*Ventral surface:* Metasternum in male feebly grooved from mesocoxa to metacoxa; groove absent in female. Abdomen shiny or dull; sterna finely punctate except for a coarsely punctured area along anterior border of sternum 1; punctures sparse on sterna 1 to 4 but dense on 5; sternum 5 without tubercles; punctures each with a fine, not easily seen, pale seta, usually most evident on fifth sternum where setae are longer; lateral setae broader and whitish and light tan in color, forming light, frequently obscure, patches.

*Legs:* Femoral teeth small and variable in size, being equal or with either proximal or distal tooth larger (one specimen with proximal tooth of mesofemora missing); legs with vestiture of white and light tan setae; metafemora annulated feebly; pro- and mesofemora without band.

*Male genitalia:* (Figs. 47 and 74). Aedeagus approximately one-half to one-third longer than wide at base and distinctly longer than aedeagal struts; outer curvature gradually widened apically; apex deeply bisinuate and with a narrow process; dorsal plate variable in width, indistinctly extending to base. Length .937-1.36 mm., width at base .536-.661 mm., aedeagal struts .550-.625 mm.

*Neotype locality:* Nashville, Tenn. Say's type locality: Mississippi.

*Neotype:* Male, June 23, 1893, H. Soltau (USNM).

*Neallotype:* Female, Riley County, Kansas, Popenoe (WPH).

*Neoparatypes:* ILLINOIS: Parker, June 8, 1913, ♂, (ISNHS); KANSAS: Topeka, 366, Popenoe, ♀, (USNM); Riley County, June 3, Kan. Ac. No. 1498, ♀, (WPH); MISSOURI: Columbia, Oct. 15, 1905, ♂, (HFS); Columbia, July 9, 1930, ♂, (UMo.); WEST VIRGINIA: French Creek, F. E. Brooks, Quaintance No. 21173, 2 ♂, 1 ♀, (USNM).

*Distribution:* Ranges from New Jersey and Pennsylvania south to North Carolina and Mississippi and west to Kansas and Missouri. Records from Arkansas, District of Columbia, Illinois, Kansas, Missouri, New Jersey, North Carolina, Ohio, Pennsylvania, Tennessee, Virginia, and West Virginia.

*Biology:* The life-history of this species has been studied by Brooks (1922). Specimens collected by Brooks at that time have been examined, and the species considered here as *retentus* (Say) is the same as the *retentus* (Say) of Brooks.

The only food plants known for this species are black walnut (*Juglans*

*nigra*) and butternut (*J. cinerea*), the latter being rarely attacked. Brooks (1922) consequently designated *retentus* (Say) the black-walnut curculio. The curculio overwinters in the adult stage, probably beneath duff on the surface of the ground. In the spring the beetles become active, attacking and feeding on leaves and tender shoots as soon as they appear. After a short time (late May and early June in W. Va.), the females begin oviposition in the young fruit, usually selecting nuts on which the female catkins have begun to wither. The eggs, when deposited in young nuts, are placed beneath the flap of skin within a crescent-shaped puncture eaten out of the side of the nut, while in half-grown nuts they are inserted in pin-prick punctures extending directly into the husk. The newly-hatched larva begins to feed from the side of the oviposition wound and, in young nuts, soon consumes the entire interior. In older nuts the feeding is done chiefly in the husk; rarely are larvae found burrowing in the tender shoots. Large nuts may contain two to three larvae, but smaller nuts generally support only one. Cannibalism occurs when several larvae are present. After the larva is about half-grown the infested nut drops to the ground, the larva continuing to feed while the nut dries and hardens.

When full grown the larva remains inactive inside the nut from 7 to 14 days before cutting its way out through the shell and entering the ground for pupation. The larvae usually leave the nuts in the morning and generally in cool weather. The pupal stage is passed 2 to 4 inches beneath the soil surface and lasts from 14 to 21 days, the adults appearing chiefly in late August. This new generation apparently feeds on the leaf petioles for a short time before going into hibernation for the winter.

Brooks (1922) states that in seasons when the walnut trees bear a light crop, a large percentage of the crop may become infested and drop, but in years of heavy fruitage the curculios only effect an unimportant thinning of the nuts. In one instance at French Creek, W. Va., Brooks collected 400 young nuts at random from four trees and found only 28% of this lot sound. In the 289 infested nuts there were 466 egg punctures. From Brooks' observation the black-walnut curculio appears more abundant and injurious in the latitude of Maryland and West Virginia than in the more northern range of the black walnut.

Parasites reared by Brooks from the larvae and pupae of the black-walnut curculio revealed three species of Diptera, *Chaetochlorops inquilina* Coq., *Cholomyia longipes* Fab., and *Fannia canicularis* L., and two species of Hymenoptera, *Triaspis curculionis* var. *rufus* (Riley) and *Thersilochus conotracheli* (Riley). The dipterous parasites were obtained in large numbers.

*Remarks:* This species was originally described by Thomas Say (1831), who characterized it as follows:

"*Cryptorhynchus retentus*. Body covered by very short, dense, prostrate hair; rostrum longer than the head and thorax; a little arcuated, punctured and on the sides lineated: thorax with two whitish undulated vittae: scutel orbicular: elytra with four elevated, acute, interrupted lines, between which are double series of impressed punctures: elevated lines obsolete on the depressed tip: thighs emarginate towards the tip and bidentate. Inhabits Mississippi. Length less than three-tenths of an inch."

Say's description does not sufficiently characterize this species to permit its positive identification. The mention of short hair (setae) and of the length are perhaps the most important points.

Leconte (1876) gave a more complete description, but had only one specimen from Kansas before him. Blatchley and Leng in 1916 again described *retentus* (Say), but their description is quite similar to that of Leconte.

The redescription by the author differs from those of Leconte and Blatchley and Leng chiefly in regard to the color of the vestiture, the size, and by the consideration of new characters. Some specimens have, under low power, the grayish cast mentioned by these writers, but under higher magnification the setae are found to be white, light tan, and brown. Other specimens have a distinct brownish hue under low magnification without a trace of gray. Both Leconte and Blatchley and Leng gave the length of *retentus* (Say) as 7 mm., but the majority of specimens on hand are below 7.0 mm., ranging from 5.6 to 6.6 mm. These variations in length at first gave an indication of size varieties, but because of the intergradations in length between the small and large specimens and because of similarity in genital structure all forms have been considered as one species. Several of these smaller specimens have a distinct brownish cast, but this appears to be due to their being freshly emerged. As the type of *retentus* (Say) has been destroyed, neotype and neoparatypes have been erected.

Both Leconte and Blatchley and Leng placed much stress on the median prothoracic callus as a means of separating *retentus* (Say) from *affinis* Boh. and the other species of Group I. This character on some specimens of *retentus* (Say) is distinct, but frequently it is obscure or else the callus extends forward as a short carina. Because of this variation and the fact that *affinis* Boh. and some of the other species in Group I may have a short carina which when feeble can easily be mistaken for a callus, this character is of little or no value. To replace it, the writer uses the sparse, fine punctation of the first four abdominal sterna to separate

*retentus* (Say), *affinis* Boh., and *hicoloriae* n. sp. as a section from *aratus* (Germ.), *elegans* (Say), and others. For further separation of *retentus* (Say), *affinis* Boh., and *hicoloriae* n. sp., see key, page 42.

*Conotrachelus affinis* Boheman

*Conotrachelus affinis* Boheman, 1837, Schönh. Gen. Spec. Curc., IV, pt. 1, p. 429; Dejean, 1835, 1837, Cat. Col., ed. 2, p. 297; ed. 3, p. 321, *n.n.*; Leconte and Horn, 1876, Rhynchophora N. A., Proc. Amer. Philos. Soc., XV, No. 96, p. 228; Blatchley and Leng, 1916, Rhynchophora N. Amer., p. 471; Mutchler and Weiss, 1925, Conotr. N. J., Circ. 87, Bur. Stat. and Insp., Dept. Agr., N. J., p. 20.

*Length:* 6.1-7.0 mm.

*Special characters:* Elytra with costal elevations not presenting an even appearance, with the median elevation of interval 3 usually the most prominent; females with a slightly curved beak that usually attains the abdomen or the posterior border of metasternum.

*Color:* Prothorax and elytra brown to dark reddish-brown, sometimes piceous.

*Head:* Semi-coarsely and densely punctate; sparse covering of brownish-yellow setae, basal setae finer; beak slightly curved in both sexes; in males curvature much sharper below antennal insertion; longer than prothorax, and much longer in female (2.6-3.5 mm.) than in male (1.9-2.0 mm.), reaching the first abdominal sternum in numerous specimens; with three lateral sulci between base and antennal insertion; sulci either distinct or faint, the median sulcus sometimes obliterated and succeeded by an irregular row of large punctures; sulci coarsely punctate; dorsal surface with an acute or broadly rounded carina extending from base to distad of middle, sometimes lacking in female; dorsal aspect distad of antennal insertion densely punctured (in female less densely, especially medially) with elongate punctures, frequently punctures appearing more like short sulci; sparse vestiture of light tan setae with a few scattered white ones; antennae inserted approximately one-third from apex in female, approximately one-fourth in male.

*Prothorax:* Sides rounded (sometimes feebly angulate) from base to approximately one-third before apex, then constricted; densely and coarsely punctate; with four faint tubercles on disc, one pair transversely at the middle, the other between median pair and base; median tubercles more prominent than posterior ones; disc on each side feebly (sometimes deeply) depressed between tubercles; with a median, longitudinal carina from anterior tubercles to apex; carina narrow and distinct or rounded and obscure, sometimes short and more of a callus than a carina; sparse vestiture of brown, light tan, and white elongate recumbent to subrecumbent setae; the white and light tan setae on each side chiefly condensed

in a sinuate line extending from near basal angle to before apex; lines approach apically but do not meet; brown setae more elongate than light tan and white ones.

*Mesoscutellum*: From dorsal aspect elongate or oval; from lateral aspect prominent (bump-like), either steeply inclined or abruptly declivent basally.

*Elytra*: Approximately two-thirds as wide as long; sides subparallel for more than half, then converging to apex; humeri prominent and obliquely rounded; basal border mesad of humeri emarginate; median elevation of interval 3 most prominent and larger than either anterior or posterior ones; costa of interval 5 either complete, or interrupted once or twice; when interrupted, median elevation most prominent; anterior elevation in one female almost obliterated; serial punctures large on basal half, finer behind the middle; sparse vestiture of brown, tan, and white elongate recumbent setae; tan and white setae condensed at postmedian band and at base of intervals 3 and 5 (the line of vestiture at base of interval 3 the most prominent); chiefly brownish setae scattered over remainder of elytra, rarely composing the central portion of the postmedian band, the band becoming less distinct when this type of seta is present.

*Ventral surface*: Metasternum usually not grooved from meso- to metacoxa in either sex; male sometimes with a faint indication of grooves. Abdominal sterna sparsely and finely punctured, except for a row of large punctures along anterior margin (occasionally in median area) of sternum 1; sternum 5 with denser punctation than sterna 1-4, without or with feeble tubercles; each puncture with a short pale seta; lateral setae broader and light tan, sometimes forming small patches on sterna 2-5.

*Legs*: Femoral teeth usually distinct on all femora, but occasionally either proximal or distal tooth is minute; sparsely covered with tan and white setae; setae condensed to form a band on metafemur at position of teeth (sometimes absent); occasionally a less distinct band subapically; pro- and mesofemora usually faintly or not annulated.

*Male genitalia*: (Figs. 48 and 75). Aedeagus approximately one-fourth longer than wide at base, and one-fourth longer than aedeagal struts; apex bisinuate and forming a broad process; dorsal plate variable in its extent; laterally, apical fourth of aedeagus distinctly but not abruptly curved ventrally. Length .775-.846 mm., width at base .548-.613 mm., aedeagal struts .625-.649 mm.

*Type locality*: "Boreal America."

*Type*: Boheman Collection; Stockholm Museum, Stockholm, Sweden.

*Plesiotypes*: ARKANSAS: Siloam Springs, July 20, 1908, Quaintance No. 5110, E. L. Jenne and S. W. Foster, ♂, ♀, (USNM); ILLINOIS: Galesburg, ♂, ♀, (ISNHS); MARYLAND: Glen Echo, June 24, 1922, J. R. Malloch, ♀ (USNM); VIRGINIA: Mt. Vernon, June 6, 1915, W. L. McAtee, ♂, (USNM); WEST VIRGINIA: French Creek, Sept. 12 and Sept. 15-16, 1920, Quaintance Nos. 21202 and 21207, reared from hickory nuts, F. E. Brooks, 4 ♂, 3 ♀, (USNM), ♂, ♀, (HFS).

*Distribution*: Ranges from New York (Buffalo) to Illinois south to Arkansas and Virginia. Recorded from Louisiana and Florida by Blatchley and Leng (1916), but these data may or may not apply to *C. hicoriae* n. sp. Records from: Arkansas, District of Columbia, Illinois, Maryland, New Jersey, New York, Pennsylvania, Virginia, West Virginia.

*Biology*: *C. affinis* Boh. and *hicoriae* n. sp. in the past have been considered as one species; the species considered here as *affinis* Boh., however, is the same as that called *affinis* Boh. by Brooks (1922) in his biological studies of the walnut and hickory curculios at French Creek, West Virginia. This synonymy is established by the fact that the accessional data of two series of curculios considered as *affinis* Boh. are: "*C. affinis* Boh., Host: Nuts of *Hicoria ovata*, numerous beetles reared from larvae attacking immature shagbark hickory nuts, nuts dropped and were collected from the ground" (French Creek, West Virginia, September, 1920, F. E. Brooks). In addition, the photograph of the adult curculio in Brook's report (Plate VI, a) is one of a female *affinis* Boh. This identification is based on the extreme length of the beak.

*C. affinis* Boh., known as the hickory-nut curculio, attacks the nuts of *Hicoria glabra*, *H. ovata*, and to some extent those of *H. alba* and *H. minima*. The adults come out of hibernation in late spring, the females commencing oviposition in late June (in W. Va.). As the curculios are especially active at nightfall, oviposition sometimes occurs after dark. Eggs are deposited in circular or crescent-shaped scars on the sides of half-grown nuts, the scars soon becoming brown or blackish and conspicuous. The resultant larvae feed singly in the nuts which drop to the ground 14 days after the larvae have begun to feed. This dropping of the green infested nuts about midsummer is the best indication of the presence of the hickory-nut curculio. In about two weeks the larvae leave the fallen nuts and pupate 1 to 2 inches below the surface of the soil, the adults issuing from the ground 30 days later (August to October). Soon after their issuance from the soil the adults go into hibernation until spring.

The larva of this curculio is attacked by several parasites. Brooks

(1922) reports two parasitic flies, *Cholomyia longipes* Fab. and *Myiophasia globosa* Towns., and two parasitic Hymenoptera, *Triaspis curculionis* var. *rufus* (Riley) and *Microgaster* sp., while Pierce (1908) records *Myiophasia aenea* Wied.

*Remarks:* *C. affinis* Boh. is closely related to both *retentus* (Say) and *hicoriae* n. sp., and confusion over their specific identities has been prevalent. As stated in the discussion of *retentus* (Say), the use of a prothoracic median callus to separate these species is of little value because of the difficulty of distinguishing between a callus and a short carina, and because of the variance occurring in the development of both these structures. The characters given in the key will best separate these species, the prominence and coloration of the postmedian elytral band usually being the most reliable external characters. Occasionally the band in *affinis* Boh. and *hicoriae* n. sp. tends to be obscure, and then a study of the other characters listed in the key is necessary.

*C. affinis* Boh. and *hicoriae* n. sp. appear to be more closely related to each other than either is to *retentus* (Say). The males of these species are distinguishable by the shape of the metaunci as listed in the key and by their aedeagi, but the females are very similar in appearance and difficult to separate. The character of the length of the antennal scape extending nearer the head capsule in *hicoriae* n. sp. than in *affinis* Boh. (Fig. 36) has been found to be the only reliable index to their specific identity. Usually the beak of *affinis* Boh. is extremely long in the female, reaching the abdomen, while that of *hicoriae* n. sp. only attains the mesocoxae. A few female specimens of *affinis* Boh., however, have beaks not attaining the abdomen, and a few specimens of *hicoriae* n. sp. exhibit beaks of the same length as these shorter "*affinis*" beaks, so this character cannot always be relied upon. If the beak of a female specimen definitely attains the abdomen, it is, without doubt, *affinis* Boh. If, on the other hand, the beak barely reaches the mesocoxae, the specimen is *hicoriae* n. sp.

The question as to whether the species here considered as *affinis* Boh. or the new species *hicoriae* n. sp. is the *affinis* of Boheman (1837) cannot be satisfactorily answered, since the type is in Stockholm, Sweden, and inaccessible at the present time. The original description and subsequent descriptions of Leconte and of Blatchley and Leng will fit both of these species. The decision to designate this species as *affinis* Boh. is based on Boheman's description of the size of *affinis* as "similar to that of *C. serpentinus* Boh." Specimens of *serpentinus* have a length of 6-7 mm., and the specimens of *affinis* Boh. described here have a similar length. On the other hand, *hicoriae* n. sp. varies from 4.4 to 7 mm. However, an examination of the type, if this is ever possible, may reverse the designations.

*Conotrachelus hicoriae* n. sp.

*Length:* 4.4-7.0 mm.

*Special characters:* Elytra with costal elevations not presenting an even appearance; median elevation of interval 3 the most prominent; females with a slightly curved beak that usually attains the mesosternum or the anterior portion of the metasternum.

*Color:* Prothorax and elytra reddish to dark reddish-brown, sometimes with small piceous or blackish areas.

*Head:* Semi-coarsely and densely punctate; sparse vestiture (sometimes moderately dense) of light tan setae; beak gradually curved to one-third before apex, curvature then more abrupt; abrupt apical curvature especially evident in male; beak sometimes straight for a short distance near middle; longer than prothorax; slightly longer in female (1.5-2.5 mm.) than in male (1.5-1.75 mm.); with three lateral sulci between base and antennal insertion; the lower sulcus distinct; median sulcus frequently indistinct and more of a row of large punctures than a sulcus; the upper sulcus also sometimes indistinct, especially apically where it evanesces into a row of large irregular punctures; male with a dorsal acute (sometimes rounded) carina from base to distad of middle; female with a rounded carina which is more distinct basally, sometimes evanescent before the middle; dorsal aspect distad of antennal insertion densely and elongately punctured in male, punctures frequently resembling small sulci because of their extreme length, those of female usually less dense and less elongate; sparse vestiture of mainly tan setae; antennae inserted approximately one-third before apex in female, one-fourth in male.

*Prothorax:* Sides rounded from base to less than one-third before apex (sometimes slightly angulate rather than rounded), then either feebly or abruptly constricted; densely and coarsely punctate; punctures more distinct laterally; disc with four tubercles, one pair transversely at the middle, the other between median pair and base; posterior tubercles less prominent than median ones, sometimes either or both pairs obsolete; a faint to distinct depression on each side between median and posterior tubercles; disc with a median, longitudinal carina (sometimes feeble) extending forward from between median pair of tubercles; carina sometimes reaching apex, sometimes evanescent before middle; sparse vestiture of light tan or yellowish, brownish-yellow, and white elongate recumbent to subrecumbent setae; yellowish and whitish setae on each side chiefly condensed in a sinuate line extending from just inside basal angle to apex; lines approach apically but do not meet; brownish-yellow setae usually more elongate than yellow or white setae.

*Mesoscutellum:* Prominent, from lateral aspect abruptly declivent basally.

*Elytra*: Nearly three-fourths as wide as long; sides subparallel for approximately half, then converging to apex; humeri prominent, obliquely rounded; base emarginate before humeri; the median elevation of interval 3 more prominent than anterior and posterior ones; interval 5 with costa interrupted once or twice; when singly interrupted break may be either anteriorly or posteriorly; occasionally the single anterior break is so feeble as to indicate a complete costa; serial punctures large, finer behind the middle; sparse vestiture of brown or yellow to white recumbent setae; whitish or light tan setae condensed in a distinct postmedian band and in a short line at base of intervals 3 and 5; both band and basal lines sometimes composed of yellowish setae or of a mixture of white and tan setae; setae of band usually distinctly denser than elsewhere; chiefly brownish-yellow or brown setae scattered over remainder of elytra, rarely included in the central portion of the postmedian band.

*Ventral surface*: Metasternum in both sexes without distinct grooves between the meso- and metacoxae. Abdominal sterna 1 to 4 sparsely, faintly, and finely punctate, except for a row of coarse punctures at basal border of sternum 1; sternum 5 more densely and usually more distinctly punctate than preceding sterna, punctation sometimes obscure, without or with faint tubercles, depressed laterally and sometimes medially; each puncture with a fine, pale reddish-brown seta which is sometimes difficult to detect, most evident on sternum 5; lateral setae broader and white, forming patches on sterna 2 to 5.

*Legs*: Femoral teeth varying from feeble to distinct; legs with sparse vestiture of white and pale tan setae; setae denser on metafemora and forming a distinct band at position of teeth, a less distinct subapical band sometimes present; pro- and mesofemora usually faintly or not at all annulated.

*Male genitalia*: (Figs. 49 and 76). Aedeagus approximately two-thirds to three-fourths as wide as long, distinctly longer than aedeagal struts; outer curvature usually with a slight indentation distad of middle; apex with a broad point but no process; dorsal plate variable in its extent; laterally, apical fifth of aedeagus is abruptly curved ventrally, sometimes more abrupt than in Fig. 76. Length .649-.673 mm., width at base .437-.512 mm., aedeagal struts .375-.524 mm.

*Type locality*: Bloomington, Illinois.

*Holotype*: Male, March 16, 1884, sifting leaves, Illinois State Natural History Survey.

*Allotype*: Female, United States National Museum Type No. 54309, French Creek, W. Va., Fred E. Brooks, Quaintance No. 7534 (USNM).

*Paratypes*: DISTRICT OF COLUMBIA, Hubbard and Schwarz, ♂,

(USNM); FLORIDA: Enterprise, May 23, C. V. Riley Coll., ♂, (HFS); Enterprise, Hubbard and Schwarz, ♀, (HFS); Monticello, June 15, 1913, bred specimens July 11 and 29, August 1, 1913, Quaintance No. 9074, J. B. Gill, 1 ♂, 2 ♀, (USNM); ILLINOIS: Monticello, August 1, 1908, ♂, (HFS); Northern Illinois, ♂, (ISNHS); KANSAS: Riley County, June 17, J. B. Norton, ♂, (WPH); Topeka, June 14 and 18, Popenoe, ♂, ♀, (USNM); LOUISIANA: Tallulah, ♀, (USNM); and Quaintance No. 4014, ♀, (USNM); NEW JERSEY: ♀, (USNM); SOUTH CAROLINA: No. Greenville Co., June 23, 1931, about 1500-2000 ft. elevation, F. Sherman, ♀, (USNM); TEXAS: Victoria, August 19, 1909, bred from pecan, McMillan, ♂, ♀, (USNM); VIRGINIA: Falls Church, July 16, 1917, Geo. M. Greene Coll., ♀, (HFS); WEST VIRGINIA: French Creek, Quaintance No. 7534, Fred E. Brooks, ♂, ♀, (USNM), ♀, (HFS); French Creek, F. E. Brooks, 2 ♀, (USNM); Morgantown, March 2, 1916, Kan. Acc. No. 3455, L. M. Peairs, 3 ♀, (WPH); West Virginia, F. H. Chittenden, ♀, (USNM).

*Distribution:* Ranges from New Jersey and Illinois south to Florida and Texas. Locality records from specimens not in type series: Arkansas (Siloam Springs); District of Columbia; Kansas (Topeka, Onaga); Louisiana (Loganport, New Iberia, Crowville, Baton Rouge); Maryland (Prince George County); New Jersey (Orange Mountain); Texas (Kerrville, Victoria); Virginia (Afton); West Virginia (French Creek).

*Biology:* This species, on the basis of specimen information, attacks the nuts of *Hicoria pecan*. J. D. Mitchell has bred specimens from green fallen pecan nuts at Victoria, Texas, and has also swept the adults from pecan trees. Data from two specimens bred by Mitchell reveal that the larvae left the green nuts about the first of August, entered the ground for pupation, with one adult issuing from the soil in about 18 days, the other in 30 days. C. E. Smith at Baton Rouge, Louisiana, records this curculio as definitely destructive to cultivated pecan. His note: "Bred from pecan, destroyed half the pecan nuts on several 11-year-old trees, larvae feed both on hull and kernel, July 26, 1934."

These data indicate that *hicoriae* n. sp. attacks *H. pecan* in much the same way as its near relative, *affinis* Boh., attacks *H. glabra*, *H. ovata*, *H. alba*, and *H. minima*. The information on the larval, pupal, and adult stages reveals that the life history and feeding habits of this species are also similar to those of *affinis* Boh. Although the available specimen data separate *affinis* Boh. and *hicoriae* n. sp. rather definitely in regard to their specific hosts, the host should not be used as a rigid criterion for the differentiation of the two species, since subsequent information may reveal similar hosts for both species. *C. hicoriae* n. sp. has been found on

peach at Siloam Springs, Arkansas, by S. W. Foster and has been collected at lights in the District of Columbia by J. R. Greeley.

*Remarks:* The taxonomic and phylogenetic discussion of *C. hicoriae* n. sp. is given under *C. affinis* Boh., page 68.

*Conotrachelus falli* Blatchley

*Conotrachelus falli* Blatchley, 1916, Blatchley and Leng, Rhynchophora N. E. Amer., p. 471.

*Length:* 4.8-5.8 mm.

*Special characters:* Prothorax with very dense, coarse, reticulate punctures, and with very sparse vestiture; proximal femoral tooth distinctly larger than distal one.

*Color:* Prothorax darker than elytra, which is reddish and black, the black chiefly present in a median transverse band.

*Head:* Coarsely and densely punctate; sparse vestiture of brownish-yellow, brown, and white setae which are finer basally; beak slightly curved to near antennal insertion, then curvature usually more distinct; beak longer than prothorax, slightly longer in female than in male; with three distinct lateral sulci between antennal insertion and base; median sulcus less distinct than other two; dorsal aspect with rounded carina from base to distad of middle; area distad of carina in female smooth and with dense, elongate, fine punctures to before the apex; area in male rough, lacking fine, dense punctation but with larger, more elongate punctures resembling small sulci; sparse vestiture of brownish-yellow and white setae from base to above antennal insertion; antennae inserted approximately one-third from apex in female, approximately one-fourth in male.

*Prothorax:* Sides slightly rounded or subparallel from base to before apex, then constricted; reticulate punctures large and deep, sometimes confluent apically; with a median, longitudinal, feebly tortuose carina, sometimes extending from basal sixth to near apex, sometimes present only on median third; length of carina variable; with very sparse vestiture of chiefly brownish subrecumbent to suberect fine setae, one to each puncture; also a few broader white and light tan (occasionally reddish-yellow) setae present along basal border medially and near basal angles.

*Mesoscutellum:* From lateral aspect abruptly declivent basally.

*Elytra:* Almost three-fourths as wide as long; sides subparallel for approximately one-half, then gradually converging apically, sometimes convergence beginning just behind the humerus; humeri obliquely rounded and not or feebly prominent; basal border mesad of humeri sometimes feebly emarginate; intervals 3, 5, 7, and 9 costate; costae

usually acute and complete, the costa of interval 3 sometimes interrupted behind the middle; serial punctures large and quadrate, smaller apically; sparse vestiture of brown, tan, and white recumbent setae, the white and light-tan setae sometimes forming a usually vague postmedian band; white setae scattered over elytra and frequently forming small patches, condensed in a prominent brief line at base of interval 3.

*Ventral surface:* Metasternum not grooved from meso- to metacoxa in either sex. Abdominal sterna coarsely and densely punctate; punctures of sternum 2 slightly smaller than those of 1; sternum 5 with finer punctures apically and without tubercles, each puncture with a fine pale amber seta; lateral setae broader and yellow or white in color.

*Legs:* Femoral teeth frequently incompletely separated; metaunci in both sexes not dentate; legs feebly annulated with white or light tan setae, the annulation progressively less distinct from meta- to profemora.

*Male genitalia:* (Figs. 50 and 77). Aedeagus slightly less than twice as long as wide, distinctly longer than aedeagal struts; prephallotremic area small; apex bisinuate with a slight process; dorsal plate faintly extended to base; laterally, ventral curvature abruptly angled one-seventh before apex; dorsal curvature also angled but before apical seventh. Length .800-.824 mm., width at base .425-.461 mm., aedeagal struts .500 mm.

*Type locality:* Porter County, Indiana.

*Type:* W. S. Blatchley Collection, June 5 (PU).

*Distribution:* Rare. Recorded only from Indiana, Virginia (Vienna, Nelson County), and Louisiana (Covington).

*Biology:* No records are available.

*Remarks:* *C. falli* Blatch. shows no close affinities to other species of Group I and, by virtue of its usually complete elytral costae, stands alone in the group. The form and size of the aedeagus, however, resembles that found in other species of the group, excepting *nivosus* Lec. and *seniculus* Lec.; and it appears that *falli* Blatch. is more closely linked to the other species in Group I than is the case with either of these two species.

#### *Conotrachelus nivosus* Leconte .

*Conotrachelus nivosus* Leconte, 1876, Rhynchophora N. A., Proc. Amer. Philos. Soc., XV, No. 96, p. 229.

*Conotrachelus plagiatus* Leconte, 1876, loc. cit., p. 233.

*Length:* 3.5-5.4 mm.

*Special characters:* Prothorax with dense, coarse, reticulate punctures, and with a dense brown and white vestiture; abdominal sterna 1-4 with scattered large punctures.

*Color:* Prothorax and elytra piceous.

*Head:* Densely but not coarsely punctate; punctures obscured for the most part by dense vestiture of brown, brownish-yellow, and white scales or scale-like setae, all of which converge toward a point distad of the middle; beak stout, strongly curved; shorter than prothorax, length equal in both sexes; from dorsal aspect wider at apical end than at base; trisulcate laterally between base and antennal insertion; the lower sulcus distinct, the median one faint or entirely lacking, the upper one varying from distinct to feeble; dorsal aspect with an obscure broad carina from base to distad of middle (usually more distinct and acute in male); carina sometimes entirely lacking; dorsal area distad of middle or distad of carina, when present, roughly punctate with fine to coarse punctures, density variable; with a dense or sparse vestiture chiefly of light brownish-yellow scales or scale-like setae, sometimes with a few scattered white ones also present; antennae inserted approximately one-third before apex.

*Prothorax:* Sides subparallel but gradually widening from base to one-third before apex, then constricted; sides sometimes rounded to apical constriction; reticulate punctures shallower on apical dorsal border; non-carinate; dense vestiture of oblong, dark brownish, brownish-yellow, and white recumbent to erect scales; brown and brownish-yellow recumbent to suberect scale-like setae intermixed over surface; white scale-like setae on each side condensed in an irregular oblique line from basal angle to middle, line sometimes dividing apically into irregular anterior and median branches, the median branches from each side uniting at the center; setae dense around borders of punctures, each of which contains one erect seta arising near its center; when bordering setae are subrecumbent or suberect and not overlapping the punctures, the latter are distinct amid the dense vestiture, most evident on median basal half; vestiture less dense on the sides.

*Mesoscutellum:* From lateral aspect abruptly declivent basally.

*Elytra:* Approximately three-fourths as wide as long; sides subparallel to approximately one-third before apex, then abruptly converging; humeri rounded and sometimes prominent; basal border feebly emarginate before humeri; intervals 3, 5, 7, and 9 at the most feebly costate; a basal elevation on interval 3 and slight subapical elevations on intervals 3, 5, 7, and 9; interval 3 also with a slight rise before the middle; serial punctures large; dense vestiture of dark brown, brownish-yellow, pale gray, and white scales or scale-like recumbent setae; whitish and pale gray scale-like setae usually covering most of basal two-thirds, except below and anterior to the humerus, where there is a small brown spot, and medially where dark brown setae cover the transverse basal area between intervals 4 and extend posteriorly one-sixth of the elytral

length; sometimes median brown area extends half the length of the elytra between intervals 3, with white and pale gray scale-like setae scattered among the brown ones; interval 1 with vestiture mainly of light brown scale-like setae; pale gray setae chiefly in a broad area posterior to humeri; apical third with dark-brown, brownish-yellow, and white scale-like setae; darker setae predominant, giving area brownish aspect.

*Ventral surface:* Metasternum not grooved from meso- to metacoxa in either sex; metapleura and sides of metasternum densely clothed with whitish scale-like setae. Abdominal sterna 1-4 shiny and sparsely punctate, with large round punctures interspersed with denser fine ones; sterna 3 and 4 with the large punctures usually alined on apical border; sternum 5 densely punctate, punctures coarse basally, becoming finer toward the apex, without tubercles; each puncture, whether coarse or fine, with a brownish-yellow, pale gray, or white seta or scale-like seta; setae scattered over sterna 1 and 2, and chiefly condensed along the sides on 3 and 4; sternum 5 with a patch of vestiture on each side of middle along basal border.

*Legs:* Distal femoral tooth frequently minute and indistinct; metaunci non-dentate in both sexes; legs usually densely covered with brown, brownish-yellow, and white scales or scale-like setae; meso- and meta-femora annulated with white scales apically, profemora feebly so.

*Male genitalia:* (Figs. 55 and 82). Aedeagus elongate, approximately two and one-half times as long as wide, and approximately three and one-half times as long as the aedeagal struts; outer curvature widened apically and indented at apical fifth; apex with a distinct process; dorsal plate obliterated except for a small triangular piece at base; distinct sclerotized plate of transfer apparatus extending beyond apex of lateral plates at middle; heavy semicircular membrane lining apical rim of pre-phallotremic area. Length .937-1.00 mm., width at base .351-.399 mm., aedeagal struts .226-.262 mm.

*Type locality:* Colorado.

*Type:* Museum of Comparative Zoology Type No. 5213, J. L. Leconte Collection (MCZ).

*Distribution:* Ranges from Indiana and Illinois to Colorado and Montana, south to Oklahoma, Texas, and New Mexico. Records from: Colorado, Illinois, Iowa, Kansas, Montana, Nebraska, New Mexico, Oklahoma, South Dakota, Texas, Wisconsin, and Wyoming.

*Biology:* This species has been taken on Russian thistle, *Salsola pestifer*, near N. Lovington, New Mexico, and N. L. Town has frequently collected it in the sandhills of Riley County, Kansas. No further biological information is available.

*Remarks:* This species belongs in Group I by virtue of its two-toothed femora, but the distal tooth is minute and can easily be overlooked. Leconte (1876, p. 233) overlooked this denticle and erected *C. plagiatu*s n. sp., but in the appendix of the same publication (p. 419) designated it a synonym of *nivosus* Lec.

Leconte in his original description of *nivosus* states that the prothorax is longer than wide. Measurements of the type, however, refute this statement, the prothorax being wider (1.65 mm.) than long (1.3 mm.).

Although placed in Group I, because of its two-toothed femora, this species shows little relationship to the other species of the group with the possible exception of *seniculus* Lec. Leconte (p. 225) terms it a transition species to his Group II (B. & L. Group IV and the writer's Group III) because of the obsolete, distal femoral tooth. *C. nivosus* Lec. does show affinities with *leucophaeatus* Fahr. on the basis of vestiture, but since it lacks the median, longitudinal furrow of the prothorax the two cannot be considered as closely related. It appears to be more a case of parallelism where similar types of vestiture have developed in distantly related groups.

#### *Conotrachelus seniculus* Leconte

*Conotrachelus seniculus* Leconte, 1876, Rhynchophora N. A., Proc. Amer. Philos. Soc., XV, No. 96, p. 227; Dejean, 1837, Cat. Col., ed. 3, p. 321, *n.n.*; Blatchley and Leng, 1916, Rhynchophora N. E. Amer., p. 472; Mutchler and Weiss, 1925, Conotr. N. J., Circ. 87, Bur. Stat. and Insp., Dept. Agr., N. J., p. 20.

*Length:* 3.7-5.0 mm.

*Special characters:* Longitudinal carina of prothorax extending from base or just before base to apex; abdominal sternum 1, excepting basal row of coarse punctures, with finer and less dense punctures than sterna 3 and 4; proximal femoral tooth much larger than distal one.

*Color:* Prothorax and elytra reddish to piceous.

*Head:* Semi-coarsely and densely punctate; sparse to moderately dense covering of brownish-yellow and tan setae; beak short, stout, and strongly curved; either shorter or but slightly longer than prothorax, equal in length in both sexes; trisulcate from above antennal insertion to base; lower sulcus broad and distinct; upper and median sulci less distinct, being obscure basally and sometimes also apically, especially the median sulcus; dorsal aspect acutely carinate; carina extending from base to above antennal insertion or ending before the middle, usually longest in male; dorsal aspect distad of carina with dense, elongate punctures which in some cases coalesce to form short sulci; vestiture of light and dark tannish setae in sulci, those arising in upper sulcus usually denser, especially basally; antennae inserted approximately one-third from tip of beak.

*Prothorax*: Sides subparallel or slightly rounded to one-fourth before apex, then suddenly constricted; densely, coarsely, and unevenly punctate; disc, in addition to depression just behind middle, with an elongate shallow depression on each side between carina and oblique line of vestiture anterior to middle; moderately dense vestiture of tan and whitish setae, tan setae usually predominating, the majority recumbent and short, some elongate and subrecumbent or suberect; lighter tan, sometimes whitish, setae condensed on each side in an oblique line extending from basal angle to apex; lines meeting apically.

*Mesoscutellum*: From lateral aspect abruptly declivent basally.

*Elytra*: Approximately two-thirds as wide as long; sides subparallel for more than half, then gradually converging to the apex; basal border feebly emarginate before the humeri, which are obliquely rounded and not prominent; intervals 3, 5, 7, and 9 feebly to moderately costate; costa of interval 5 complete, or interrupted once or twice, usually complete or with feeble indication of an interruption anteriorly; costa of interval 7 sometimes extremely feeble; that of interval 9 sometimes extending onto humerus basally; serial punctures coarse, less distinct distad of middle; with a moderate to dense covering of brownish and tannish or pale tannish, sometimes whitish, oblong or elongate recumbent setae, the lighter tan and sometimes the whitish ones condensed in a usually faint postmedian band; color range of setae varying from dark brown to white; each interval with a row of white or brownish suberect setae; similar setae arising from serial punctures; setae when brown not very evident, sometimes visible only on a small area; other times present over most of elytra, their prominence variable; setae when white conspicuous; whitish setae sometimes abundant, the entire vestiture then lighter in color and the postmedian band distinct.

*Ventral surface*: Metasternum not grooved from meso- to metacoxa in either sex. Abdominal sternum 2 with punctures denser and coarser on basal two-thirds than those of sternum 1; apical third of sternum 2 with fewer punctures; sternum 5 without tubercles and densely punctate, punctures along basal border resembling those of preceding sternum, punctures finer apically; each puncture with an elongate seta; lateral setae usually broader and white and tan in color, those in central areas of sterna usually less evident, pale amber to whitish; apical borders of sterna 3 and 4 usually bearing a few conspicuous suberect setae, the latter sometimes present on sternum 2.

*Legs*: Metaunci not dentate in either sex; femora with setae denser on apical third and lighter in color than those basally, especially on meta-femora, where the apical band is usually most evident.

*Male genitalia:* (Figs. 56 and 83). Aedeagus elongate, three times as long as wide at base, and eight and one-half times as long as the aedeagal struts, gradually widened apically; apex without a process; dorsal plate elongate; sclerotized plate of transfer apparatus projecting beyond apex of dorsal plate; apical end of prephallotremic area lined with a heavy membrane which extends basally at the middle. Length 1.11-1.18 mm., width at base .312-.350 mm., aedeagal struts .125-.137 mm.

*Type locality:* "Middle States."

*Lectotype*, hereby designated: Museum of Comparative Zoology Type No. 5223-2, J. L. Leconte Collection (MCZ).

*Lectoparatypes:* Museum of Comparative Zoology Type Nos. 5223-3 and 5223-4; "Western States," J. L. Leconte Collection (MCZ); Museum of Comparative Zoology Type No. 5223-5, Texas; J. L. Leconte Collection (MCZ).

*Distribution:* Ranges from Quebec and New England to Michigan and Kansas south to Mississippi and Florida," Blatchley and Leng (1916). Extended to Arizona by Leng (1920). Range herein further expanded westward to California and to Nebraska. This is the most widely spread species in the genus. One specimen has the locality label "Tacoma, Washington," but as there are no further data on the label, and since no *Conotrachelus* has ever been reported from that region (Northern California, Oregon, and Washington), the author feels that this record should be confirmed before being accepted. Although probably over five hundred specimens have been examined, none have been found occurring north of New Jersey to substantiate Blatchley and Leng's (1916) statement of its occurrence in Quebec and New England. Possibly these records of northern distribution are the result of misidentifications, since in the past *seniculus* Lec. has been confused with *elegans* (Say). Mr. C. A. Frost, who has collected extensively in Massachusetts, has informed the writer that he knows of no authentic record of this species from New England. Records from: Alabama, Arizona, Arkansas, California, Delaware, District of Columbia, Florida, Illinois, Indiana, Iowa, Kansas, Kentucky, Louisiana, Maryland, Mississippi, Missouri, Nebraska, New Jersey, North Carolina, Ohio, Oklahoma, Pennsylvania, South Carolina, Tennessee, Texas, Virginia.

*Biology:* Chittenden (1898) first noticed the work of *C. seniculus* Lec. on the roots of *Amaranthus*, but unfortunately misidentified the species as *elegans* (Say). In 1924 the same writer, however, corrected this error of identification. At this time he gave *seniculus* Lec. the common name of "Amaranth curculio."

The following specimen data substantiate Chittenden's records that

Amaranth is the common host: "In crown of *Amaranthus*" (Bentonville, Ark., A. J. Ackermann); "feeding on roots of *Amaranthus* sp." (Baton Rouge, La., C. E. Smith and N. Allen); "host *Amaranthus*" (Thornville, Ohio, C. R. Neiswander); "feeding in roots of *Amaranthus hybridus* (green pigweed)" (Falls Church, Va., R. A. St. George); and "collected on pigweed" (Moorehaven, Fla., J. E. Graf and K. E. Bragdon).

Chittenden (1924) found a heavy infestation of larvae on the roots of cultivated amaranth in the first week in September at Washington, D. C. Three weeks later the majority of the insects were in the pupal stage, and on September 28 the first adult emerged. Chittenden found that the larvae were most numerous on mature plants, frequently injuring the stems as well as the roots. In 1898 the same writer reared adults from the roots of *A. retroflexus* as early as August 18 in Washington, D. C. *C. seniculus* Lec. has also been collected on bean stalks, alfalfa, grass, and in cotton bolls, and has been observed feeding on spinach. No information is available on the activities of this species in the winter, spring, and early summer.

From specimen records the writer believes that this species is attracted to lights more readily than any of the other *Conotrachelus* considered in this report. Records show that *seniculus* Lec. has been collected "at lights" or "in light traps": Tempe and Phoenix, Arizona; District of Columbia; Homestead, Florida; Elizabethtown, Illinois; Douglas County, Kansas; Gueydon, Louisiana; Plummer's Island, Maryland; Charleston, Missouri; Crowley, North Carolina; Durant, Oklahoma; Nashville, Tennessee; Plano and Victoria, Texas; Falls Church and Maywood, Virginia; Webster Springs, West Virginia. This species has also been taken in Japanese Beetle traps at St. Louis, Missouri.

*Remarks:* *C. seniculus* Lec. is easily distinguished from the other species in Group I by the distinct longitudinal carina and discal depressions of the prothorax. Unfortunately, it has been confused with *elegans* (Say), which not only lacks the prominent prothoracic carina but has an abdominal punctation quite distinct from that of *seniculus* Lec. Specimens of *seniculus* Lec. usually are dirty, and the prothoracic sculpture consequently obscure, and possibly this is the reason for its misidentification as *elegans* (Say). Frequently specimens of *posticatus* Boh. are also labelled *seniculus* Lec., but this is due to a lack of examination, since *posticatus* Boh. has only one femoral tooth and belongs to Group II.

In the Leconte Collection at Cambridge, the first cotype of *seniculus*, Type No. 5223-1, "Middle States," is a specimen of *aratus* (Germ.) and consequently does not fit the original description of *seniculus* Lec. Therefore, the second specimen of the cotype series has been designated as the lectotype. Leconte did not designate types, and those in the Leconte Col-

lection were indicated by Henshaw. This fact releases Leconte from the inaccuracies sometimes found in the type specimens of his collection.

On the basis of the male genitalia, *seniculus* Lec. and *nivosus* Lec. are definitely isolated from the other species of Group I. In both, the transfer apparatus is heavily sclerotized and projecting into the prephallotremic area, and in both the dorsal plate of the aedeagus is of unusual form. In *seniculus* Lec. (Fig. 56) this plate is elongate and directly connected to the lateral plates along its entire length, while in *nivosus* Lec. (Fig. 55) it is lacking except for a small triangular basal piece. In all the other species of Group I, the dorsal plate is separated from the lateral plates apically by membranous areas, and the transfer apparatus does not project into the prephallotremic area.

### *Conotrachelus elegans* (Say)

*Cryptorhynchus elegans* Say, 1831, Desc. N. A. Curc. New Harmony, Indiana, p. 18, in Writings of Thomas Say, ed. Leconte, 1859, p. 283.

*Conotrachelus elegans* (Say) Boheman, 1837, Schönh. Gen. Spec. Curc., IV, pt. 1, p. 428; Leconte and Horn, 1876, Rhynchophora N. A., Proc. Amer. Philos. Soc., XV, No. 96, p. 228; Blatchley and Leng, 1916, Rhynchophora N. E. Amer., p. 472; Mutchler and Weiss, 1925, Conotr. N. J., Circ. 87, Bur. Stat. and Insp., Dept. Agr., N. J., p. 20.

*Length:* 3.8-5.1 mm.

*Special characters:* Abdominal sterna 1-4 coarsely and densely punctate; interpunctate areas of sterna 1 and 2 usually not larger than the diameters of the punctures.

*Color:* Prothorax and elytra reddish and black, black of elytra frequently centered in basal discal half, the red apically; the apex sometimes black; derm beneath postmedian band usually reddish; discal area not always distinct.

*Head:* With dense semi-coarse punctures; sparsely covered with tan and white setae; beak in male but slightly longer than prothorax; curvature moderate until near apex, then more abrupt; beak in female elongate (Fig. 39), distinctly longer than prothorax; curvature slight but even from base to tip, longer (1.55-1.97 mm.) than in male (1.20-1.45 mm.); beak in both sexes with three lateral sulci from base to distad of middle, sulci varying in distinctness; upper and median sulci sometimes shallow and ill-defined; dorsal aspect broadly to acutely carinate from base to distad of middle; surface distad of carina with dense elongate punctures; punctures more distinct in female and sometimes less dense; with sparse tan and white setae arising from lateral sulci; antennae inserted approximately one-third from apical tip in female, approximately one-fourth in male.

*Prothorax:* Sides gradually rounded from base to near apex, then

constricted; sides sometimes subparallel for a short distance; with dense, coarse punctures, the punctures less evident apically and sometimes confluent; disc usually without tubercles, but occasionally two feeble pairs present, one transversely at middle, the other between median pair and base; disc sometimes depressed on posterior two-thirds; if tubercles are evident, depressed areas are between the median and posterior pairs; usually non-carinate but occasionally with a vague, feeble ridge from middle to before base; sparse vestiture of light reddish-yellow to white elongate recumbent to subrecumbent setae; light-colored setae condensed on each side into an oblique line from just inside basal angle to near apex; lines approach apically but do not meet, sometimes obscure.

*Mesoscutellum*: Prominent, from lateral aspect abruptly declivent basally.

*Elytra*: Between two-thirds and three-fourths as wide as long; sides subparallel for over half, then gradually converging to apex; humeri rounded, not prominent; basal border only feebly emarginate before humeri; intervals 3, 5, 7, 8, and 9 feebly to moderately costate; median elevation of interval 3 usually longer and more prominent than the others; anterior interruption sometimes so slight as to indicate completeness basally; costa rarely definitely complete anteriorly; costa of interval 5 either complete or interrupted posteriorly, with occasionally a faint indication of anterior interruption; serial punctures coarse on basal half of elytra, deeper and closer together anteriorly; sparse vestiture of pale white, white, reddish-yellow, and tan recumbent setae; lighter tan and white setae condensed in a definite postmedian band and sometimes in a short line at base of intervals 3 and 5.

*Ventral surface*: Metasternum in male grooved from meso- to metacoxa; groove absent in female. Abdominal sterna 1 and 2 usually with punctures as dense as in Fig. 33, but sometimes less dense; sterna 3 and 4 sometimes with punctures smaller than those of 1 and 2; sternum 5 more finely punctate apically than other sterna, without tubercles or with faint broad protuberances; each puncture with a fine, pale reddish seta; lateral setae broader, tan and white, sometimes forming small patches along the sides on sterna 2 to 5.

*Legs*: Femoral teeth usually distinct, sometimes feeble; either tooth may be larger; in males pronotum sometimes feebly dentate, metapectus sometimes tridentate (Fig. 25); legs with sparse vestiture of pale white, white, or tannish setae, sometimes dense on apical third of femora, especially metafemora.

*Male genitalia*: (Figs. 51 and 78). Aedeagus nearly twice as long as wide and distinctly longer than aedeagal struts; sides gradually tapering to apex, which has only extremely feeble sinuations; laterally, the ven-

tral and dorsal curvatures gradually approaching apically, the aedeagal cavity being shallow. Length .687-.750 mm., width at base .355-.406 mm., aedeagal struts .343-.450 mm.

*Neotype locality:* Jefferson Barracks, Missouri. Say's type localities: New Jersey and Florida.

*Neotype:* Male (USNM).

*Neallotype:* Female, Carbondale, Illinois; May 18, 1910, on hickory (ISNHS).

*Neoparatypes:* ILLINOIS: Algonquin, Nason, ♂, ♀, (DEUI); Northern Illinois, 3 ♀, (ISNHS), ♂, 2 ♀, (HFS); Villa Ridge, June 4, 1892, Ac. Nos. 18657, 18658, McElfresh, ♂, ♀, (ISNHS); Dubois, May 10, 1904, Ac. No. 34664, Taylor, jarred from plum, ♂, (ISNHS); Cedar Lake, June 20, 1892, Ac. No. 18356, Shiga, and Hart, ♀, (ISNHS); Oakwood, May 8, 1927, Frison, ♀, (ISNHS); IOWA: Mt. Pleasant, June 17, 1926, ♂, (WPH); KANSAS: Riley County, Popenoe, ♀, (USNM); MARYLAND: Plummer's Island, May 24, 1914, L. L. Buchanan, ♀, (USNM); MICHIGAN: Detroit, Hubbard and Schwarz, ♂, (USNM); NEW JERSEY: Booton, June 11 and 16, 1901, Geo. M. Greene Coll., ♂, ♀, (USNM); New Jersey, Chittenden Coll., ♀, (HFS); Clifton, August 8, 1906, R. Godfrey, Geo. M. Greene, ♂, (USNM); New Foundland, 5-30, Ed. A. Bischoff Coll., ♀, (USNM); Orange Mt., Ed. A. Bischoff Coll., ♀, (USNM); and New Jersey, Chicago Field Museum Coll., ♀, (HFS); NORTH CAROLINA: Raleigh, May 17, 1940, pecan 255, R. C. Barnes, ♂, (HFS); TEXAS: ♀, (WPH); Victoria, June 7, 1910, Hunter No. 3789, J. D. Mitchell, ♀, (HFS); VIRGINIA: Falls Church, July 4, 1919, L. L. Buchanan, ♂, (USNM); Nelson County, August 2, 1927, W. Robinson, ♀, (USNM); WEST VIRGINIA: French Creek, F. E. Brooks, ♂, ♀, (WPH).

*Distribution:* "Ranges from Massachusetts to Michigan and Missouri, south to Florida." Blatchley and Leng (1916). Range extended north to Ontario, west to Kansas and Nebraska, and southwest to Texas. Records from: Alabama, Illinois, Indiana, Iowa, Kansas, Louisiana, Maryland, Massachusetts, Michigan, Missouri, Nebraska, New Jersey, New York, North Carolina, Ohio, Ontario (Toronto), Pennsylvania, South Carolina, Tennessee, Texas, Virginia and West Virginia.

*Biology:* The biological status of *C. elegans* (Say) has been uncertain in the past because of misidentifications. As discussed under *C. seniculus* Lec., Chittenden (1898) mistook that species for *elegans* (Say). His subsequent correction (1924) has cleared up much, but unfortunately not all, of the confusion concerning the host plants of *elegans* (Say).

Say (1831) originally collected *elegans* (Say) on *Pinus rigida*, while Hamilton (1895) reports it as common on hickory, the larvae living on

the leaves. Ulke (1902) also reports this species on hickory. Pierce (1907a), quoting Packard, states that *elegans* (Say) lays its eggs in the partly rolled up leaves of pignut hickory (*Hicoria glabra*) in late May, and during oviposition cuts off the leaves causing them to hang down, wither, and turn black. Hunter and Pierce (1912) list *elegans* (Say) as the pecan gall weevil, attacking the galls and nuts of hickory, and Pierce (1916) states: "*C. elegans* Boheman is a very important enemy of nuts. In Texas the first generation breed in the petioles and new shoots of hickory (*H. alba*). Later individuals are found commonly in the leaf galls of *Phylloxera devastatrix* on pecan (*H. pecan*), and still later the species is bred from nuts of various species of *Hicoria*." Champlain and Knull (1921) at Westbury, N. Y., record the adults as damaging the stems of hickory in feeding and in making egg punctures, and the larvae as working in the shoots and leaf stems, causing them to wilt and fall. Mutchler and Weiss (1925) term *elegans* (Say) the "pig-nut leaf curculio" and state that it has been wrongly recorded as attacking pecan.

The specimen records on *elegans* (Say) are as follows: "bred from pecan leaf galls" (Victoria, Texas, J. D. Mitchell); "bastard hickory" (Beaumont, Texas); "*Hicoria pecan*" (Victoria, Texas); "on *Verbesina virginica*" (Victoria, Texas, R. A. Cushman); "bred from *Phylloxera devastata* gall, *Hicoria pecan*" (Victoria, Texas, J. D. Mitchell); "in cotton field" (Victoria, Texas, W. E. Hinds); "bred from *Phylloxera* gall on hickory" (W. Chester, Pa.); "bred from *Phylloxera* gall" (Baton Rouge, La., T. H. Jones); "on hickory" (Carbondale, Illinois); "collected on pecan" (Raleigh, N. C., R. C. Barnes); and "jarred from plum" (Dubois, Illinois, Taylor).

A correlation of the literature records with the specimen records reveals that in some instances *elegans* (Say) probably has been confused with *aratus* (Germ.) or *tibialis* n. sp. The data listed by Pierce (1916), concerning the first generation, and by Champlain and Knull (1921) indicate feeding, ovipositional, and breeding habits similar, if not identical, to those given by Brooks (1922) for *aratus* (Germ.) or *tibialis* n. sp.\* Consequently, unless corroborative evidence is obtained, the writer is inclined to question the validity of these records as applying to *elegans* (Say).

The specimen records definitely establish this species as breeding in the galls of *Phylloxera* on pecan and hickory. They also indicate its occurrence on hickory, but whether the curculios were actually breeding on or in some part of the tree or were in search of galls is not clear. The literature records of Pierce (1907a) and Hunter (1912, 1916), con-

\*One paratype of *tibialis* n. sp. was collected at Westbury, N. Y., by Champlain on *Hicoria*, May 25, 1916. Champlain and Knull (1921) state that the adults of *elegans* (Say) were first observed at Westbury on May 25. As these writers do not mention *aratus* (Germ.) and as *tibialis* n. sp. was not known, this specimen very likely represents the species they considered as *elegans* (Say).

cerning the ovipositional and larval food habits of *elegans* (Say) on the leaves and nuts of hickory, should be further substantiated before being considered authentic for the species.

As *elegans* (Say) has been reared from galls on pecan, the common name "pecan-gall curculio" appears to be more applicable than the name "pig-nut leaf curculio."

There is one specimen record of this species being attracted to a trap light.

*Remarks:* The species which Say (1831) had in mind when he originally described *elegans* has never been satisfactorily determined. The destruction of Say's types, as in the case of *retentus* (Say), has caused the definition of *elegans* (Say) to be principally a matter of common interpretation among coleopterists. This is due, not only to the fact that Say's original description can now be applied to several species, but also to the tendency of biological or geographic varieties to occur within the species. Say's original description is as follows:

"Body dull piceous, more or less varied with brown or blackish; rostrum sulcated, carinate, piceous: antennae rufous: thorax lobed at the eyes; punctured; an obsolete, oblique, cinerous line each side proceeding to the posterior angles; elytra with four somewhat elevated, acute lines, the exterior ones uniting behind; interstitial spaces wide, with double series of punctures, obsolete behind; behind the middle is a more or less dilated common space, narrower at the suture than on the lateral margin; on this spot the inner elevated line is interrupted, and the line is also depressed or interrupted toward the base; thighs two-toothed, somewhat annulated with piceous and blackish.

"Length less than  $\frac{1}{5}$  of an inch.

"Var. a. somewhat cinereous.

"Var. b. Paler piceous; larger."

Specimens of *C. aratus* (Germ.) or *seniculus* Lec. would fit equally well Say's description. Say has indicated the occurrence of varieties, but since these appear to be based chiefly on color and size, too much significance cannot be placed upon them.

Leconte (1876) gave a more complete description of *elegans* (Say), and in his key distinguished it from *aratus* (Germ.) on the appearance of the postmedian elytral band, this being distinct in *elegans* (Say) and obscure in *aratus* (Germ.). This difference is a comparative one and sometimes of little value unless specimens of both species are available.

Blatchley and Leng (1916) redescribed *elegans* (Say), but their characterization was similar to that of Leconte's. These writers, in their key, separated *elegans* (Say) and *aratus* (Germ.) by abdominal characters in addition to the comparative distinction of the postmedian band. In *elegans* (Say), according to Blatchley and Leng (1916), all the ventral

abdominal segments are closely and rather coarsely punctate and the fifth sternum is without tubercles, while in *aratus* (Germ.) the first and second sterna are very coarsely but not densely punctate and the fifth is finely, more densely punctate and bears two distinct tubercles. These characters of Blatchley and Leng hold in most cases, but there is variation. The abdominal punctuation occasionally tends to be less dense on the first and second sterna in *elegans* (Say), and the fifth sternum may have slight tubercles, while *aratus* (Germ.) may lack distinct tubercles and have a moderately dense abdominal punctuation of the first and second sterna. Such variations lead to confusion, especially when a specimen of either species is lacking for comparison. The characters set forth in the writer's key appear to be stable and will serve for identification with only one specimen on hand. These characters and the description have been based on the examination of the thirty-three specimens listed under neotype and neoparatypes. All specimens have shown a uniformity with regard to the key characters and to the genital structures. Since the original type specimens have been destroyed and since there is a definite need for a criterion upon which to base this species, the writer hereby designates a male specimen from Jefferson Barracks, Missouri, H. Soltau collection (United States National Museum) as the neotype. This specimen and its neoparatypes are what is commonly interpreted as *elegans* (Say).

In the southeastern region particularly, *elegans* (Say) appears to be the center of a large complex of forms, all of which, though closely related to it, show variations from it. The majority of specimens that the writer has examined from the northeastern area, however, have been the typical *elegans* (Say). One male from Massachusetts, considered as belonging to the complex, appears from its genitalia to be more closely related to *aratus* (Germ.).

*C. elegans* (Say) is closely related to *hayesi* n. sp. and *aratus* (Germ.). The latter also appears to be the center of a complex which may be shown to be closely linked to the *elegans* group when the full complement of the species and the variations of both complexes have been investigated.

*Conotrachelus hayesi* n. sp.

*Length:* 4.7-5.1 mm.

*Special characters:* Abdominal sterna 1 and 2 with a moderately dense punctuation, that is, with distinct non-punctate areas present which sometimes are two or more times the diameters of the punctures; post-median elytral band obscure; beak in female with distance (a) approximately three or more times distance (b).

*Color:* Prothorax and elytra uniformly piceous or blackish in female, reddish and black mixed in male.

*Head:* Densely and semi-coarsely punctate; with a sparse covering of light tan and white setae; beak slender (Figs. 37 and 40) and slightly curved, curvature in male more abrupt at position of antennal insertion; beak distinctly longer than prothorax, longer in female (1.9-2.0 mm.) than in male (1.45-1.50 mm.); beak in both sexes distinctly trisulcate laterally from base to above antennal insertion, the median sulcus sometimes evanescent basally; dorsal aspect with a distinctly acute or rounded carina, which in male extends to approximately one-third to one-fourth before apex, and in female to approximately one-half before apex; dorsal aspect distad of carina with dense elongate punctures which are more elongate in male than in female; from dorsal aspect, beak in female feebly constricted in area between antennal insertion and apex, no constriction in this area in male; sparse vestiture of white and tannish setae arising from sulci; antennae in male inserted approximately one-fourth from tip of beak, in female between one-third and one-half, nearer one-third in one specimen, nearer one-half in the other two.

*Prothorax:* Sides sometimes gradually rounded from base to apex, or outline more sharply convergent anterior to middle than posteriorly; coarsely and densely punctate; punctures shallower and several confluent near apex; disc non-carinate and without tubercles; with a sparse vestiture of brownish-yellow and white recumbent to subrecumbent setae, the white setae forming a vague oblique line on each side from inside of basal angle to apex; lines sometimes absent.

*Mesoscutellum:* Prominent, from lateral aspect abruptly declivent basally.

*Elytra:* Approximately two-thirds as wide as long; sides subparallel for more than half, then gradually converging to the apex; basal border feebly emarginate before humeri, the latter not prominent; intervals 3 and 5 feebly to moderately costate; costa of interval 5 interrupted feebly near the base; costa of interval 9 sometimes so feeble behind the middle that it appears to be slightly interrupted; serial punctures coarse from base to before vague postmedian band, smaller apically; sparse vestiture of brownish and whitish recumbent setae; brownish setae chiefly aligned on the non-costate intervals; white setae chiefly on slopes of costae and in punctures, slightly more abundant between middle and posterior elevations of third intervals; brownish setae denser behind middle and with white setae forming a vague, ill-defined, postmedian band.

*Ventral surface:* Metasternum not grooved between meso- and metacoxae in either sex. Abdominal sterna with punctures moderately coarse in female, between fine and coarse in male, especially on sternum 2; sternum 5 and usually 4 more densely punctate than 1 and 2 and sometimes more than 3; sternum 3 may or may not be more densely punctate

than sterna 1 and 2; sternum 5 laterally depressed, depressions less distinct in male, the latter with a median depression, without or with feeble tubercles; each puncture with a pale amber or whitish fine seta; lateral setae broader and white.

*Legs:* Femoral teeth more prominent in female; metaunci of male dentate (Fig. 28), those of female not dentate; femora and tibiae with a sparse covering of yellow and white setae; setae denser on apical portion of metafemora at position of teeth.

*Male genitalia:* (Figs. 52 and 79). Aedeagus elongate, two and one-half times as long as wide at base and approximately four times as long as the aedeagal struts, sides subparallel, slightly widened at apex; apex feebly bisinuate; dorsal plate merging with lateral plates approximately one-third from base. Length 1.197-1.209 mm., width at base .461 mm., aedeagal struts .187-.286 mm.

This species is named for Professor W. P. Hayes, Department of Entomology, University of Illinois.

*Type locality:* Northern Illinois.

*Holotype:* Male, No. 1, Illinois State Natural History Survey.

*Allotype:* Female, Northern Illinois, United States National Museum Type No. 55124.

*Paratypes:* Northern Illinois; No. 2, ♂, (ISNHS); Henry County, Iowa; April 24, 1939, ♀, (HFS); West Carroll, Louisiana, 1-14, under bark, ♀, (USNM).

*Distribution:* Recorded only from above localities.

*Biology:* No data are available for this species.

*Remarks:* *C. hayesi* n. sp. belongs between *elegans* (Say) and *aratus* (Germ.) resembling in certain respects both of these species. The shape and length of the rostrum is similar to *elegans* (Say), but the abdominal punctation, structure of the meso- and metaunci in the males, and the distinctness of the postmedian elytral band more closely resemble *aratus* (Germ.). The similarity in external characters, however, is not correlated with male genital likenesses. The aedeagus of *hayesi* n. sp. is distinctly different from that of either *elegans* (Say) or *aratus* (Germ.) as can be seen by a comparison of Figs. 51, 52, and 53. In a lateral view, however, the aedeagus of *hayesi* n. sp. (Fig. 79) does resemble that of *elegans* (Say) (Fig. 78) more closely in contour than that of *aratus* (Germ.) (Fig. 80). All specimens of *aratus* (Germ.) or *elegans* (Say), however, even though larger in size than *hayesi* n. sp. have the aedeagus distinctly shorter than this species. The marked genital differences between *hayesi* n. sp. and both *elegans* (Say) and *aratus* (Germ.) indicate that there are probably other unknown species which would fall into this group.

*Conotrachelus aratus* (Germar)

*Cryptorhynchus aratus* Germar, 1824, *Insectorum Species Novae*, Halle, p. 283.

*Conotrachelus aratus* (Germ.) Schönherr, 1837, *Schönh. Gen. Spec. Curc.*, IV, pt. 1, p. 457; Boheman, 1845, *Schönh. Gen. Spec. Curc.*, VIII, pt. 2, p. 26; Leconte, 1876, *Rhynchophora N. A.*, *Proc. Amer. Philos. Soc.*, XV, No. 96, p. 228; Blatchley and Leng, 1916, *Rhynchophora N. E. Amer.*, p. 473; Mutchler and Weiss, 1925, *Conotr. N. J.*, Circ. 87, *Bur. Stat. and Insp., Dept. Agr.*, N. J., p. 20.

*Length*: 4.35-5.75 mm.

*Special characters*: Femoral teeth evident in both sexes.

*Color*: Prothorax and elytra piceous, black, and red mixed.

*Head*: Semi-coarsely punctate; punctures sometimes indistinct; with a sparse vestiture of whitish and tannish setae; beak stout and curved (Figs. 38 and 41), curvature sometimes abrupt apically in male; as long as or longer than prothorax, subequal in length in both sexes; beak trisulcate laterally between base and antennal insertion; lower sulcus always distinct, others varying from distinct to obscure, especially the median sulcus which sometimes is replaced by large punctures; dorsal aspect carinate from base to beyond middle; carina in female sometimes evanescent before or at the middle, feeble or moderately prominent, more acute in male; aspect distad of antennal insertion with fine elongate punctures; punctation moderate to dense, usually more so in male, the surface appearing minutely sulcate; sparse vestiture of tan and white setae arising from sulci; antennae inserted approximately one-fourth from tip in male, nearer one-third in female.

*Prothorax*: Sides gradually rounded from base to near apex, then constricted; densely and coarsely punctate; punctures less distinct apically; with four feeble tubercles on disc, one pair transversely at the middle, the other between median pair and base; median pair most evident and present even when posterior set is obsolete; disc on each side sometimes depressed between median and posterior tubercles; with either a feeble carina from between median tubercles apically or non-carinate; sparse vestiture of elongate tan and white recumbent to subrecumbent setae, white or light tannish setae on each side forming a vague, curved line from inside of basal angle to apical border; lines approach apically but do not meet.

*Mesoscutellum*: From lateral aspect usually sloping steeply basally or abruptly declivent.

*Elytra*: Approximately one-third longer than wide; sides subparallel for more than half, then gradually converging to the apex; humeri rounded, variable in prominence; basal border emarginate (sometimes feebly) before humeri; intervals 3, 5, and 7 feebly to moderately costate;

elevations of interval 3 feeble to moderate, the median one most prominent; costa of interval 5 usually interrupted twice, interruptions sometimes feeble; costa occasionally complete posteriorly, elevations usually feeble; serial punctures feeble to distinct; sparse vestiture of brown, brownish-yellow, tan, and white recumbent setae; relative abundance of each type variable; when whitish setae are well scattered, abundant, and mixed with light-tannish ones, the elytra have a grayish cast; when brownish-yellow and brown setae predominate, a tannish to brownish hue is present; lighter setae condensed in an ill-defined postmedian band and possibly in a brief line at base of interval 3.

*Ventral surface:* Metasternum in male grooved from meso- to metacoxa; grooves absent in female. Abdomen: Punctuation of sterna 1 to 5 varying from moderately dense (Fig. 34) to dense, punctures coarse, those of sternum 1 usually larger than those of sterna 2-5; sterna 3 and 4 usually more densely punctate than 1 and 2; sternum 5 more densely punctured than sterna 1-4, punctures becoming finer apically, usually with two distinct tubercles on either side of the middle apically, tubercles sometimes feeble; each puncture with an elongate, usually fine, pale amber seta; lateral setae broader and white; vestiture usually most evident on sternum 5.

*Legs:* Femoral teeth small; femora and tibiae with sparse vestiture of tan and white setae, most frequent on distal third of metafemora, sometimes forming a band.

*Male genitalia:* (Figs. 53 and 80). Aedeagus one-fourth to one-third longer than wide at base and approximately one-fourth longer than aedeagal struts; apex abruptly narrowed to form a prominent process; dorsal plate broad apically and narrowed at the base; basal border may have a smoother curve than that shown in Fig. 53. Length .796 mm., width at base .531 mm., aedeagal struts .600 mm.

*Type locality:* Kentucky.

*Type:* Zool. Univ. Mus., Halle, a. S.

*Plesiotypes:* ALABAMA: Mobile County, H. P. Loding, ♀ (USNM); ILLINOIS: Urbana, September 9, 1925, V. G. Smith, ♂. (CAF); KANSAS: Riley County, April 24, May F. Marlatt, ♂, 2 ♀, (WPH), ♀, (HFS), ♀, (USNM); Topeka, June 13, Popenoe, ♂, (USNM); Onaga and Wilson County, June 7 and April 23, Wickham, 2 ♀, (USNM); MISSISSIPPI: Poplarville, April 27, 1926, pecan L401, W. B. Tate, ♀, (HFS); Wiggins, March 24, 1929, hickory petioles, J. P. Kislando, ♀, (USNM); TEXAS: Columbus, May 6, Hubbard and Schwarz, ♀, (USNM).

*Distribution:* Ranges from Massachusetts to Illinois and Kansas, south to Alabama and Mississippi, and southwest to Texas.

*Biology:* Since *aratus* (Germ.) in the past has been confused with *tibialis* n. sp., the biological information given under *tibialis* n. sp. (p. 93) can probably be applied to *aratus* (Germ.) as well. Two specimen records indicate *Hicoria* as a probable host: "pecan" (Poplarville, Miss., L. B. Tate) and "hickory petioles" (Wiggins, Miss., J. P. Kislando).

*Remarks:* *C. aratus* (Germ.) is another North American species about which a great deal of confusion has arisen. In this instance the type, although possibly still in existence in Europe, is not available, especially at the present time, to American workers.

Germar (1824) described *aratus* with Kentucky as the type locality. It was not again characterized until 1876. At that time Leconte (1876, p. 228) stated that he referred, with some hesitation, to this species a specimen from Texas, 4 mm. in length. Leconte distinguished this specimen of *aratus* (Germ.) from all other members of Group I by the punctuation of the abdominal sterna: first and second very coarsely but not densely punctured, third and fourth strongly punctured, fifth finely and more densely punctate with two distinct tubercles. Blatchley and Leng (1916, p. 473) gave a similar description, asserting that *aratus* (Germ.) could easily be distinguished from allied species by the abdominal punctuation and the presence of the two tubercles on the fifth sternum. Mutchler and Weiss (1925), in a descriptive key, characterized this species by its color, vestiture, and elytral sculpture, all characters of questionable value in this section of the genus.

From this summary, it appears that the abdominal punctuation and tuberculation are the principal characters to rely upon. Germar's original description is general and can also be applied to *elegans* (Say) or *retentus* (Say). Several of the specimens on which the author's redescrptions are based agreed with the type of abdominal punctuation and tuberculation set forth by Leconte. Others, however, show variations, although the specimens are all the same species. Of four specimens from the same locality and of the same date, three show distinct tubercles on the fifth sternum, but the fourth is only feebly tuberculate. The abdominal punctuation also shows similar variation; in specimens from the same locality some show the not-dense punctuation specified by Leconte and Blatchley and Leng, while others have a dense punctuation. Since such variations occur in specimens from the same locality, the writer feels that he is justified in considering these specimens to be *aratus* (Germ.) even though their structures sometimes do not fit exactly the specifications set forth by previous authors. Another character of Leconte and Blatchley and Leng that does not fit some of these specimens is that concerning the non-interruption anteriorly of the elytral costae of the fifth intervals. These

costae are usually interrupted at this point, but they are too variable in form in this section of Group I to be used as definite taxonomic indicators; therefore, such a digression is not significant.

Leconte and Blatchley and Leng also used the prominence of the postmedian elytral band as a means of separating *elegans* (Say) and *aratus* (Germ.). This character is of value, but with only one specimen on hand its use is sometimes limited.

Germar (1824) gave the size of *aratus* as similar to that of *Notaris acriduli*, which varies in length from less than 4 to 5 mm. The specimens interpreted as *aratus* (Germ.) vary from 4.35 to 5.75 mm. Leconte (1876) gave the size of *aratus* (Germ.) as 4 mm., but a measurement of his Texas specimen places the length at 4.35 mm.

*C. aratus* (Germ.) is most closely related to *tibialis* n. sp., from which it is separated by the characters given in the key.

*Conotrachelus tibialis* n. sp.

*Length:* 4.5-5.75 mm.

*Special characters:* Males with proximal femoral tooth absent or obsolete; sides of prothorax sometimes distinctly bulging near apical third.

*Color:* Prothorax and elytra reddish and black mixed.

*Head:* Semi-coarsely and densely punctate; with a sparse vestiture of light tan and pale white setae; beak stout, curved, longer than prothorax (rarely shorter in male), and longer in female than in male; male beak with three lateral sulci from base to above antennal insertion; median sulcus less distinct than others and with large, deep punctures; dorsal face of beak moderately to acutely carinate from base to distad of middle; tip distad of carina densely and finely punctate, punctures so dense that tip appears finely sulcate; female beak with less distinct sulci and with only a feeble carina; sulci and carina sometimes lacking; dorsal surface distad of antennal insertion with fine distinct punctures, moderate to dense in composition; beak in both sexes sparsely covered with white and tan setae which arise from sulci when these are present or from punctures which replace sulci; antennae inserted approximately one-fourth from tip in male, nearer one-third in female.

*Prothorax:* Distinctly wider than long; sides usually rounded, sometimes with a distinct bulging near the apical third; with dense coarse punctures, less evident apically, occasionally with a feeble indication of two tubercles on disc behind middle; sometimes with a feeble longitudinal carina on disc from middle to one-fourth before apex; disc frequently with two depressions behind middle; vestiture sparse, consisting of white and tan recumbent to subrecumbent setae, usually one to a puncture;

lighter setae condensed on each side to form a faint sinuate line from inside of basal angle to apex; lines approach apically but do not meet.

*Mesoscutellum*: From lateral aspect abruptly declivent basally.

*Elytra*: Approximately one-third longer than wide; sides subparallel for more than half, then gradually converging to apex; basal border with feeble emarginations inside of humeri, the latter rounded and not prominent; intervals 3 and 5 feebly to moderately costate; elevations of interval 3 feeble; interval 5 with costa either once or twice interrupted; when only singly broken, interruption either anterior or posterior; costa sometimes acute and occasionally complete; serial punctures large and quadrate anterior to postmedian band, smaller at band and behind it; sparse vestiture of mostly brownish and tannish recumbent setae; whitish setae usually present but not as abundant as darker ones; light tan and light brown setae condensed in a postmedian band, usually vague, rarely distinct; a faint line of light tan setae at base of third interval.

*Ventral surface*: Metasternal grooves absent in both sexes. Abdominal sterna 1-4 coarsely punctate; punctures numerous, sometimes dense; those of sterna 3 and 4 usually slightly denser than those of 1 and 2; sternum 5 more densely and finely punctate than others, punctures on basal third approaching in size those of preceding sternum; punctation on apical half obscure in female; two, usually distinct, tubercles on apical third in male, those of female feeble to distinct; each puncture with a fine, pale amber seta; lateral setae broader, white and pale-white in color, forming obscure patches on sterna 2-5.

*Legs*: Females with femoral teeth small but evident; protibiae usually distinctly mucronate proximad of unci; mucrones present on meso- and metatibiae but difficult to detect; femora and tibiae of both sexes with a sparse vestiture of light tan and whitish setae which are denser on apical third of metafemora than elsewhere.

*Male genitalia*: (Figs. 54 and 81). Aedeagus one-fourth to one-third longer than wide at base, and one-fourth to one-third longer than aedeagal struts; sides slightly widened apically; apex bisinuate and with a distinct process; dorsal plate variable in its extent; basal border of aedeagus sometimes a smooth curve instead of angled as shown in Fig. 54. Length .562-.649 mm., width at base .387-.425 mm., aedeagal struts .379-.476 mm.

*Type locality*: Mendenhall, Mississippi.

*Holotype*: Male, United States National Museum Type No. 54310, April 18, 1911, J. E. Boggan, S:3042 (USNM).

*Allotype*: Female, Mendenhall, Mississippi, April 18, 1911, J. E. Boggan, S:3042 (USNM).

*Paratypes*: Iowa: Mt. Pleasant, May 7, 1930, Jones, ♂, (WPH);

Iowa City, Wickham, ♀, (HFS); ILLINOIS: Southern Illinois, H. Soltau, ♂, (USNM); KANSAS: Wilson County, April 23, 1896, on hickory buds, ♀, (MSC); LOUISIANA: New Iberia, June 6, 1896, Coll. H. Soltau, ♀, (USNM); No. 4676<sup>01</sup>, other data illegible, ♂, (USNM); MASSACHUSETTS: Southboro, May 30, 1923, C. A. Frost, ♀, (USNM); MISSISSIPPI: Poplarville, May 29, 1926, pecan L401, W. B. Tate, ♂, (USNM); MISSOURI: Jefferson Barracks, Coll. H. Soltau, ♂, (USNM); NEW YORK: Westbury, L. I., May 25, 1916, *Hicoria*, A. B. Champlain, ♀, (USNM); WEST VIRGINIA: French Creek, May 29, 1920, F. E. Brooks, Quaintance No. 21101, jarred from branches of young hickory trees, identified as *C. aratus*, ♂, (HFS), ♀, (USNM).

*Distribution:* Ranges from Massachusetts and New York to Iowa and Kansas, south to Mississippi and Louisiana.

*Biology:* As both *tibialis* n. sp. and *aratus* (Germ.) have been considered as *aratus* (Germ.) in the past, it is difficult to evaluate the available biological literature. From specimen records both species appear to have the same host, *Hicoria*, and in all probability their life histories are somewhat similar. Brooks (1922) gives an account of the biology of *aratus* (Germ.), but on the basis of the information on two paratypes (Quaintance No. 21101) the species with which he worked was *tibialis* n. sp. In this study Brooks' data, therefore, are discussed under *C. tibialis* n. sp. One definite record, however, does not eliminate the possibility that Brooks also worked with *aratus* (Germ.), since the two species have the same host and are very similar in appearance. Consequently, the writer feels that Brooks' data may also, in the absence of more definite information, be applied equally well to *aratus* (Germ.).

*C. tibialis* n. sp. has been recorded only from hickory, Brooks (1922) listing it as attacking *Hicoria minima*, *H. ovata*, *H. alba*, *H. glabra*, and *H. pecan*. The tender tips and leaves of these trees usually wither and drop as a result of the egg-laying and feeding of the curculio. No instance of serious loss from its activity, however, has as yet been reported. In the spring, soon after the hickory buds open, the curculios emerge from hibernation, the females commencing oviposition when the shoots are but a few inches long. Each egg is placed in a shallow cavity at the side of an elongate slit made in the bark of the twigs and leaf petioles. During this period of oviposition the adults also feed on the young growth. The egg hatches about a week after deposition, the resultant larva usually feeding in the center of the bulb-like swelling at the base of the leaf petiole. Sometimes it also mines the pith of the shoots and leaf stems. Larval activity occurs in the spring and early summer when the growth is new and tender. When full grown the larvae burrow one-half to two inches below the surface of the soil for pupation. Two to three weeks

later (midsummer) the adults issue from the ground. In autumn they go into hibernation until spring.

Brooks (1922) states that during the period of his investigations at least 50% of the larvae died from parasitism. Three parasitic flies, *Myiophasia globosa* Towns., *Cholomyia longipes* Fab., and *Chaetochlorops inquilina* Coq., as well as an unidentified species of hairworm, were reared from larvae.

The work of *tibialis* n. sp. has sometimes been ascribed to *C. elegans* (Say).

*Remarks:* The remarkable form of the protibiae and the aedeagal differences easily separate the males of *tibialis* n. sp. from *aratus* (Germ.). The females, on the other hand, are difficult to distinguish, and the characters given in the key appear to be the best indicators of specific distinction. The writer is not completely satisfied with these characters since occasionally a female specimen turns up which by their use might possibly be referred to either species.

## GROUP II

The species listed under this group were divided into two groups by Leconte and Horn (1876, p. 421) and Blatchley and Leng (1916, p. 467). The characters which these writers used for the separation of the two groups were based on the structure of the beak, which in one group was slender and much longer than the head and thorax, while in the other it was rather stout, curved, and scarcely longer than the head and thorax. From a study of the species in these two groups it appears that the above writers had before them when they erected these groups only females of several of the species in the long-beaked group. In addition, by examination of Leconte's types, it has been ascertained that he had only the females of *adspersus* Lec. and *naso* Lec. before him, and this fact in all probability led to his arrangement of the key which Blatchley and Leng have followed. The key of these workers is valid when females alone are considered. Unfortunately, the males of the long-beaked group have snouts that resemble those of the short-beaked group, and this fact nullifies the validity of the key. Therefore, it has been necessary to consolidate these two groups into one in order to obtain a key which would avoid the confusion introduced by the use of the beak as a group characteristic.

In addition, the division of Group II into two parts by these authors placed the species of *naso* Lec. and *posticatus* Boh. in different groups. Examination of these species shows that the form of the aedeagus, shape of the mesosternum, prothoracic sculpture, abdominal punctation, shape of the male metaunci, and elytral sculpture (especially the presence of

the costate first and second elytral intervals in the males) are extremely similar in both species and indicate a very close relationship between the two. Consequently, it appears to the writer that to put these two species in separate groups would be wholly ignoring an obvious affinity.

In the past, Group II has been known as the "*crataegi* group." As *crataegi* Walsh is phylogenetically isolated from the other species in the group (as well as from all other known species of United States *Conotrachelus*) this designation is an unfortunate misnomer. As in Group I, reference to any one species as typifying the group should be omitted.

Group II is here characterized by the presence of one femoral tooth, but a second feeble tooth (denticle) is usually present in *cribricollis* (Say); relative length of first and second funicular segments of antennae variable; prothorax wider than long, longitudinally carinate or not carinate; mesoscutellum from lateral aspect abruptly declivent basally; elytral intervals 3, 5, 7, and 9 acutely costate, feebly convex, or flattened; costae, when present, usually complete, intervals never with abrupt elytral elevations; vestiture of recumbent setae, scales, or scale-like setae; suberect to erect setae usually present on elytral intervals and sometimes in prothoracic punctures; recumbent setae not condensed in a broad postmedian band; metasternum in male never grooved from meso- to metacoxa; male sometimes with dentate metaunci; aedeagus with a dorsal membrane (except in *crataegi* Walsh), frequently with an apical process, and with the transfer apparatus a complex of sclerotized bars.

#### KEY TO SPECIES OF GROUP II

1. Humeri truncate and dentiform; prothorax prominently and broadly elevated in the median discal area; aedeagus with dorsal plate, the latter cleft apically (Fig. 57).....*crataegi* Walsh, p. 96
- 1- Humeri not truncate or dentiform; prothorax never prominently elevated in the median discal area; aedeagus with a dorsal membrane, never as shown in Fig. 57..... 2
2. First funicular segment of antenna as long as the second and third combined; beak distinctly longer than the prothorax; aedeagus as shown in Fig. 58; length 6.5-7.2 mm.....*adspersus* Leconte, p. 99
- 2- First funicular segment of antenna usually subequal to the second only, rarely equal to the second and third combined; if so, the specimens will be less than 3.2 mm., have the beak and prothorax subequal in length, and have the aedeagus as shown in Fig. 63..... 3
3. Prothorax with a distinct longitudinal, median carina; mesosternum with anterolateral angles truncate and prominent..... 4
- 3- Prothorax not carinate; mesosternum never with anterolateral angles truncate and prominent..... 6
4. Profemoral tooth absent or obsolete, the apical ventral emargination of the profemur (viewed posteriorly) broad (Fig. 96).....*naso* Leconte, p. 101
- 4- Profemoral tooth distinct, the apical ventral emargination of the profemur deep and more acute (Figs. 97 and 98)..... 5

5. Male: metaunci dentate; antennal insertion almost reaching lateral apical emargination of beak (Fig. 108); protibia bearing on its apical margin, adjacent to uncus, long, slender, curved, light-tannish setae; setae much longer than uncus and usually in a tuft, sometimes also present on mesotibia; elytral interval 2 not costate; aedeagus as shown in Figs. 99 and 103; female: metaunci not dentate; beak slender (Fig. 101), the distance (a) between lateral apical emargination of beak and anterior margin of ball of antennal scape three or more times the distance (b) between dorsal and ventral surfaces of beak at position of antennal insertion (Figs. 101 and 105).....*carinifer* Casey, p. 104
- 5- Male: metaunci dentate; a distinct area between antennal insertion and lateral apical emargination of beak (Fig. 109); apical margin of protibia without a tuft of long, curved, light-tannish setae; elytral interval 2 usually distinctly costate anterior to the apical declivity; aedeagus as shown in Figs. 60 and 87; female: metaunci not dentate; beak moderately stout (Fig. 102), the distance (a) less than twice the distance (b).....*posticatus* Boheman, p. 106
6. Vestiture of oblong to elongate, recumbent setae, never of broad scales; elytral intervals each with a row of short or long suberect setae; prothorax with sparse vestiture, punctures clearly evident; aedeagus either sharply convex (Fig. 88) or trilobed apically (Fig. 62)..... 7
- 6- Vestiture of broad scales; elytral intervals each with a row of subrecumbent, recurved setae; prothorax with dense vestiture concealing punctures; aedeagus as shown in Figs. 63 and 90.....*recessus* (Casey), p. 109
7. Prothorax with 11 to 13 punctures from base to apex along the median line; punctures dense and deep but not forming longitudinal ridges; abdominal sterna not roughly punctate; sterna 2 to 5 never with numerous suberect elongate setae; aedeagus distinctly convex (Fig. 88), not trilobed apically (Fig. 61).....*geminatus* Leconte, p. 111
- 7- Prothorax with 6 to 8 large punctures from base to apex along the median line; punctures dense and extremely deep, forming frequent tortuose longitudinal ridges; abdominal sterna roughly punctate; sterna 2 to 5 with scattered, usually numerous, suberect elongate setae; aedeagus not convex (Fig. 89), trilobed apically (Fig. 62).....*cribricollis* (Say), p. 114

### *Conotrachelus crataegi* Walsh

*Conotrachelus crataegi* Walsh, 1864, Proc. Bost. Soc. Nat. Hist., IX, p. 311; Leconte and Horn, 1876, Rhynchophora N. A., Proc. Amer. Philos. Soc., XV, No. 96, p. 230; Provancher, 1877, Faune Ent. Can. I Col., p. 528; Blatchley and Leng, 1916, Rhynchophora N. E. Amer., p. 474; Mutchler and Weiss, 1925, Conotr. N. J., Circ. 87, Bur. Stat. and Insp., Dept. Agr., N. J., p. 20.

*Length:* 3.75-5.75 mm.

*Special characters:* Crest of prominent median prothoracic elevation carinate from behind middle to before apex; sides of elytra converging from just behind base to apex; mesosternum emarginate and with prominent anterolateral processes; abdominal sterna 3 and 4 usually with only a few shallow punctures, surface frequently smooth.

*Color:* Prothorax and elytra reddish-brown, piceous, and black mixed.

*Head:* Densely punctate; with a sparse to moderately dense covering of mostly tan scales, but also a few white ones; beak moderately stout

and curved; longer than prothorax, slightly longer in female than in male; trisulcate laterally between base and antennal insertion; upper and median sulci evanescent basally, distinct and prominent apically; dorsal surface with a feeble rounded carina at the most; surface distad of antennal insertion with fine, elongate punctures, moderately dense to dense in composition; beak with a sparse to moderately dense vestiture of light-brown and white setae arising in the sulci; antennae inserted approximately one-fourth to one-third before apex; first and second funicular segments subequal in length and longer than any of the remaining segments; second segment longer than segments five and six combined; sixth and seventh segments globose.

*Prothorax*: Sides subparallel until near apex, then abruptly constricted; point of constriction sometimes tuberculate; coarsely and densely punctate; punctation usually obscured to a large degree by dense vestiture; disc occasionally with a tubercle on each side of median elevation; moderately dense to dense vestiture of white, grayish, and tan scales and scale-like setae, the tannish vestiture in basal discal area and along lateral surfaces, the white usually covering the apical half of the disc and forming a broad curved band to the basal angle on each side; tannish scale-like setae sometimes the most abundant, so that above pattern is altered, the white scale-like setae merely forming on each side a curved line from basal angle to median elevation, the remainder of prothorax being tannish; suberect dark tan and white setae scattered amid the predominant recumbent vestiture; vestiture less dense on lateral surfaces.

*Elytra*: More than four-fifths as wide as long; sides gradually converging from base to apex; convergence more abrupt one-fourth or less before the apex; basal border feebly emarginate before humeri; the latter truncate, prominent, and with their apical angles dentiform; intervals 3, 5, 7, and 9 usually strongly costate; costae usually complete, but those of intervals 3 and 5 sometimes showing feeble interruptions; costa of interval 3 sometimes flattened both anteriorly and posteriorly, that of interval 5 anteriorly; interval 8 with a brief basal ridge which, by its acute junction with the humerus, causes the latter to appear dentiform at its apical angle; occasionally a true denticle develops at this point; serial punctures large, smaller apically; punctures usually obscured by vestiture; moderately dense vestiture of tan, grayish, and white, oblong and tapering, scales or scale-like setae; vestiture pattern variable; tannish vestiture usually predominant with the scale or scale-like setae varying from light to dark tan (brownish), so that elytra sometimes are mottled in appearance; white scales or scale-like setae occasionally abundant mesad of the humeri and in basal discal area; white elongate or scale-like setae arising from the punctures and alined sparsely but distinctly on the flattened

intervals, also present on costate intervals but arrangement less uniform, those of punctures usually much shorter than those of flattened intervals, these setae quite prominent when remainder of vestiture is dark tan.

*Ventral surface:* Abdominal sterna 1 and 2 coarsely and sparsely to moderately punctate; punctures of sternum 2 slightly coarser than those of 1 but less dense in composition; sometimes apical third of 2 is non-punctate and smooth; sterna 1 and 2 also with smaller punctures interspersed among the large coarse ones; sterna 3 and 4 with punctures much smaller than those of the preceding sterna, surface frequently smooth with only a faint indication of punctation, punctures in some cases distinct; sternum 5 more finely punctate than sterna 1 to 4, punctures moderately dense to dense, with two faint tubercles and with lateral and median depressions; sterna with a covering of tan (sometimes with an orange tinge) and white setae; vestiture denser on sterna 1 and 2 than on 3, 4, and 5, except laterally on 3, 4, and 5 where distinct patches are formed.

*Legs:* Femoral tooth distinct; metaunci non-dentate in both sexes; femora and tibiae with a moderately dense to dense vestiture of recumbent tannish oblong scales or scale-like setae, among which suberect white and tan elongate setae frequently arise.

*Male genitalia:* (Figs. 57 and 84). Aedeagus approximately twice as long as wide at base; aedeagal struts long, sometimes three-fourths as long or equal in length to aedeagus; apex feebly bisinuate; dorsal plate distinct, narrow on basal half, then widened abruptly, cleft at apex, feebly extended to base; transfer apparatus with a pair of stout lateral bars. Length .750-.875 mm., width at base .375-.399 mm., aedeagal struts .625-.812 mm.

*Type locality:* Illinois.

*Type:* Male, Museum of Comparative Zoology Type No. 8434, J. L. Leconte Collection (MCZ).

*Distribution:* "Ranges from New England to Michigan and Iowa, south to Georgia," Blatchley and Leng, (1916). Range extended north to Ontario and west to Kansas and Texas. Records from: Arkansas, Connecticut, Georgia, Illinois, Iowa, Kansas, Louisiana, Maryland, Massachusetts, Mississippi, Missouri, New Jersey, New York, Ohio, Ontario, Pennsylvania, Texas, Vermont, Virginia, West Virginia, Wisconsin.

*Biology:* *C. crataegi* Walsh is an important economic pest of quince, being considered by Slingerland and Crosby (1930) and by Peairs (1941) as the most serious insect enemy of this fruit. Infested quinces are misshapen and knotty. The life-history, summarized from Slingerland (1898), Wellhouse (1922), and Peairs (1941), is as follows: The curculio overwinters as a larva, 2 to 3 inches below the surface of the

soil. Pupation occurs in the spring, the adults emerging from the ground in June and July and feeding on the growing fruit and, to some extent, on the leaves. The females gouge pits in the fruit and deposit one egg in each pit. The resultant larvae feed on the pulp, one larva commonly consuming about one-half of the entire pulp before dropping to the ground (August and October) and entering the soil. There is one generation in a year, and the insect may spend from 7 to 11 months in the soil.

Slingerland (1898) reports that *crataegi* Walsh breeds in pear, peach, quince, and hawthorn. Wellhouse (1922) states that it is common on all native hawthorns. Host records from specimens have been limited to these plants.

*Remarks:* *C. crataegi* Walsh is common in Illinois. The presence of the dentiform humeri and the gradual tapering convergence of the elytra from their wide base to the apex easily distinguishes *crataegi* Walsh from its allied species, none of which appear very closely related to it. The aedeagus of this species does not bear any resemblance to the aedeagi of the other species studied. In form and general structure *crataegi* Walsh is also distinct from those species not included in this study which would fall into this group. It appears to be clearly different from, and not closely related to, any other known *Conotrachelus* in the United States.

Walsh's original description was published in the Proceedings of the Boston Society of Natural History, Vol. IX, for the year 1863, but the actual date of publication was March, 1864 (*loc. cit.*, bottom of page 305). Previous citations for this species have indicated 1863 as the date of publication, which is incorrect. Walsh's description was also published in *Prairie Farmer*, n. s., Vol. 12, No. 2, July 11, 1863, p. 21; but as this agricultural journal is not a technical publication, this earlier description is invalid.

#### *Conotrachelus adspersus* Leconte

*Conotrachelus adspersus* Leconte, 1876, *Rhynchophora* N. A., *Proc. Amer. Philos. Soc.*, XV, No. 96, p. 230.

*Length:* 6.5-7.25 mm.

*Special characters:* Beak not sulcate; rarely a feeble lateral sulcus in male dorsad of antennal groove; prothorax, at the most, with only a faint indication of a median longitudinal carina; mesosternum without antero-lateral processes.

*Color:* Prothorax and elytra a uniform dark red, sometimes piceous.

*Head:* Densely and finely punctate; with a sparse covering of tan and white scales or scale-like setae; beak straight to antennal insertion, then distinctly curved; beak longer than prothorax, longer in female, sometimes

reaching the base of the abdomen (in female more than 3 mm. in length, in male less than 2.5 mm.); surface with fine elongate punctures varying from sparse to dense; dorsal surface in male sometimes finely carinate from base to above antennal insertion; beak bare except for a few setae basally; antennae in male inserted approximately one-half or less from apex, in female distinctly more than one-half; third funicular segment distinctly longer than the fourth.

*Prothorax*: Sides subparallel from base to middle, then gradually converging apically; with dense, moderately coarse punctures; disc non-tuberculate; dorsal surface with a moderately dense vestiture of light-tan and white elongate or scale-like recumbent setae; setae sparse in median discal area from base to middle, sometimes from base to apex, so that denser lateral vestiture forms a broad band on each side; bands may or may not unite apically; lateral surfaces with sparse vestiture.

*Elytra*: One-fourth longer than wide; sides subparallel for approximately half, then gradually converging to the apex; basal border feebly emarginate before humeri; the latter not prominent, obliquely rounded; intervals 3 and 5 feebly costate from approximately one-half to apex, anterior to middle usually non-costate, costae becoming more evident apically, sometimes acute, especially that of interval 3; interval 7 feebly costate, costa sometimes extending from base to apex; serial punctures coarse, sometimes hidden by vestiture; with a moderately dense vestiture of white and tan or pale gray recumbent scales or scale-like setae; the tan or pale gray setae condensed in intervals 2, 4, 6, and 8 to form vittae, the white ones aggregated in small patches between the serial punctures, the arrangement of setae and scales giving elytra a very mottled appearance, the white scales also condensed basally near humeri and at interval 3; each interval sometimes with a row of subrecumbent white setae.

*Ventral surface*: Mesosternum usually straight anteriorly, sometimes feebly and broadly emarginate. Abdominal sterna with a moderately dense to dense punctation; punctures fine to moderately coarse; those of sterna 1 and 2 sometimes less dense than those of the sterna 3, 4, and 5; sternum 5 sometimes more coarsely punctate than sterna 1 to 4, especially apically, without tubercles and usually not depressed; sterna sparsely clothed with elongate setae, chiefly white, but also a few light tan ones; lateral setae broader and forming small patches on sterna 3, 4, and 5.

*Legs*: Femoral tooth usually feeble, that of metafemur most evident; metaunci not dentate in either sex; femora and tibiae with a sparse vestiture of light tan and white scale-like setae; metafemora sometimes with a narrow annulation at position of tooth.

*Male genitalia*: (Figs. 58 and 85). Aedeagus approximately two and one-half times as long as wide at base and more than twice the length of

the aedeagal struts; sides subparallel to apical sixth, then converging; apex feebly bisinuate; dorsal area membranous and V-shaped at apex; a pair of short U-shaped bars under membrane (bars not shown in Fig. 58). Length 1.43 mm., width at base .574 mm., aedeagal struts .601 mm.

*Type locality:* Kansas.

*Type:* Female, Museum of Comparative Zoology Type No. 5216, Popenoe, J. L. Leconte Collection (MCZ).

*Distribution:* Limited to Kansas principally. Also taken in Illinois, and Drury records it from Ohio. Records from: Illinois and Kansas.

*Biology:* The only available biological data are two specimen records: "on flowers" (Riley Co., Kansas, Towne) and "on *Helianthus*" (Kansas).

*Remarks:* This large species with its conspicuously mottled elytra is readily distinguished from other species by the characters given in the key. Its closest relative is *invadens* Fall, a unique species from El Paso, Texas, which resembles *adspersus* Lec. in form but differs from it chiefly by the presence of erect elytral bristles and by the third funicular segment of the antennae being scarcely as long as the fourth.

### *Conotrachelus naso* Leconte

*Conotrachelus naso* Leconte, 1876, Rhynchophora N. A., Proc. Amer. Philos. Soc., XV, No. 96, p. 231; Blatchley and Leng, 1916, Rhynchophora N. E. Amer., p. 475; Mutchler and Weiss, 1925, Conotr. N. J., Circ. 87, Bur. Stat. and Insp., Dept. Agr., N. J., p. 21.

*Conotrachelus cinereus* Van Dyke, 1930, New Rhynchophora from Western North America, Pan-Pac. Ent., VI, No. 4, p. 158 (new synonymy).

*Length:* 4.8-6.6 mm.

*Special characters:* Femoral tooth feeble or obsolete, that of meta-femur most evident; prothorax densely but not deeply punctate; female beak slender and in repose reaching base of abdomen, the distance (a) 7 to 9 times the distance (b), with antennal insertion approximately one-half before the apex; male beak stouter, in repose only reaching metasternum, with antennal insertion one-fourth from apex.

*Color:* Prothorax and elytra dark reddish-brown; elytra with black blotches which sometimes are quite numerous.

*Head:* Densely punctate; sparsely covered with light tan and white elongate setae; basal setae finer; beak in male distinctly trisulcate laterally between base and antennal insertion, dorsal surface with a feeble rounded carina from base to distad of middle, surface distad of antennal insertion with fine, elongate punctures, dense along lateral areas, punctures forming small sulci; beak in female shiny, trisulcate laterally between base and antennal insertion, lower sulcus distinct, median and upper sulci fre-

quently feeble, the upper one sometimes being marked only by a row of closely-set, fine, elongate punctures, not carinate, dorsal tip distad of antennal insertion with fine elongate punctures, subapically dense and covering the entire surface, near antennal insertion sparse and arranged along lateral edges, the median area being smooth; sparse vestiture of pale setae present in the sulci, female beak frequently bare; second funicular segment of antennae elongate, usually longer than first and subequal to or longer than segments four and five combined, sixth and seventh not globose, sides subparallel or tapering toward base.

*Prothorax*: Sides smoothly rounded from base to apex, constricted just before apex; occasionally curvature slight so that sides appear subparallel; very densely punctate; punctures large but shallow, prominently confluent apically; with a distinct longitudinal median carina from base to apex; without tubercles; extremely sparse vestiture of pale tan and white (sometimes pale pink), recumbent to subrecumbent, elongate setae; a few broader white setae frequently forming four small spots transversely behind the middle, the discal spots usually the most evident.

*Elytra*: Approximately one-third longer than wide; sides distinctly subparallel for more than half, then gradually converging to apex; basal border emarginate before humeri; the latter not prominent, obliquely rounded; intervals 3, 5, 7, and 9 acutely and completely costate; possibly a very feeble indication of an interruption anteriorly on costae of intervals 3 and 5; males usually with intervals 1 and 2 also acutely and completely costate, that of interval 1 usually extending from base to apical declivity, that of 2 attaining the apical declivity but usually evanescent anteriorly, sometimes barely evident; females with interval 1 sometimes feebly costate; serial punctures coarse and closely set; with a sparse to moderately dense vestiture of pale tan or brown, tan, and white recumbent elongate setae, frequently tapering; white setae scattered in small aggregates along costae and at base of intervals 3 and 6, denser and sometimes forming a narrow transverse band postmedianly; pale brown and tan setae chiefly in non-costate intervals, the tannish setae sometimes replacing the white ones at base of intervals 3 and 6; the above pattern varying, depending on density of setae; each interval set with short, suberect, pale tan to brown, sometimes white, blunt-tipped setae which are sometimes difficult to detect.

*Ventral surface*: Metasternum protuberant anteriorly, deeply emarginate, and with anterolateral projections. Abdominal sterna with dense, medium-sized, deep punctures; fifth sternum usually depressed medianly, sometimes tuberculate; each puncture with a pale tan, amber, or white elongate seta; setae both recumbent and suberect, sometimes almost entirely suberect, giving venter a "bristly" appearance.

**Legs:** Metaunci in male dentate, those of female not dentate; legs with a sparse covering of white and tannish setae; vestiture denser on apical area of metafemora; the latter sometimes annulated.

**Male genitalia:** (Figs. 59 and 86). Aedeagus twice as long as wide and twice as long as aedeagal struts; sides subparallel to apical fifth, then converging to form a distinct apical process; inner curvature variable in form basally; dorsal membrane sinuately V-shaped; transfer apparatus consisting of a complex of bars of which the elongate lateral pieces are the most distinct; lateral and ventral pieces protruding into prephallogtremic area, especially the lateral ones; laterally, aedeagus has an extreme basal extension of the basal ventral angle. Length .974-1.18 mm., width at base .474-.536 mm., aedeagal struts .375-.461 mm.

**Type locality:** Texas.

**Type:** Female, Museum of Comparative Zoology Type No. 5222, J. L. Leconte Collection (MCZ).

**Distribution:** "Ranges from New York to Indiana, south to Florida and Texas," Blatchley and Leng (1916). Range extended northwest to Minnesota and west to Iowa. Records from: Arkansas, District of Columbia, Florida, Illinois, Iowa, Kansas, Louisiana, Maryland, Michigan, Minnesota, Mississippi, New Jersey, North Carolina, Oklahoma, Pennsylvania, Texas, and Virginia.

**Biology:** *C. naso* Lec. is recorded by Pierce (1907a) as breeding in the fruit of *Crataegus* and in the acorns of post oak (*Quercus stellata*) and live oak (*Q. virginiana*); and by Brooks (1910) as breeding in acorns of white (*Q. alba*) and chestnut oak (*Q. montana*). *C. naso* Lec. attacks the acorns of many species of *Quercus*. According to data taken from specimens, it has been bred from acorns of: *Q. virginiana* (Georgetown, S. C.; Pas Christian, Miss.; Arlington, Va.; and Victoria and Boerne, Texas); *Q. velutina* (Boerne, Texas; District of Columbia; and Arkansas); *Q. brevifolia* (Alvah, Fla.); *Q. ruba* and *Q. pedunculata* (District of Columbia); *Q. alba* (Ruston, Ia.; Arlington, Va.); *Q. stellata*, *Q. durandii*, and *Q. nigra* (Victoria, Texas). In addition, *naso* Lec. has been taken "on cotton" at Valdosta, Georgia; McCloud, Oklahoma; Victoria and Pt. Loraca, Texas; and "on dogwood" in Riley County, Kansas.

At French Creek, W. Va., Brooks (1910) reports that the eggs are deposited in the acorns in the fall, sometimes a dozen or more to an acorn. The resultant larvae leave the acorns the subsequent winter and spring and pupate in the ground, the adults appearing about midsummer. Pierce (1907a) states that J. D. Mitchell at Victoria, Texas, obtained 266 larvae from 167 acorns of *Q. virginiana* between October 7 and 14. These larvae entered the ground immediately; the first pupa appeared March 7, the

first adult April 2. These data of Brooks and Pierce appear to be the only information available on the life-history of this species.

*C. naso* Lec. has been collected "at lights" at Glen Echo, Maryland; Raleigh, North Carolina; College Station, Texas; and Maywood, Virginia.

*Remarks:* *C. naso* is closely related to *posticatus* Boh., *carinifer* Csy., and *integer* Csy., a species which is confined to the southwest and therefore not considered in this study. Nothing definite can be stated concerning the interrelations of the three species studied, other than that all three form a compact group. This is evidenced by the form of their aedeagi (Figs. 59, 60, and 99), rostral characteristics, and habitus, as well as by similarities in host plants. The order in which these three species are placed in this report is not intended to show their exact phylogenetic arrangement.

Dr. E. C. Van Dyke has informed the writer that *cinereus* Van Dyke is but an extreme of *naso* Lec., being somewhat darker, and having the elytra more sharply narrowed and more prominently costate.

### *Conotrachelus carinifer* Casey

*Conotrachelus carinifer* Casey, 1892, Ann. N. Y. Ac. Sci. VI, p. 440.

*Length:* 4.75-5.70 mm.

*Special characters:* Prothorax with dense deep punctures, which have distinct sides; beak in male trisulcate laterally, in female unisulcate, the other sulci obsolete; humerus with an oblique, usually prominent, patch of yellow or tannish setae; metafemoral tooth distinct.

*Color:* Elytra dark reddish-brown with a few small black areas; prothorax piceous to black, darker than elytra.

*Head:* Densely punctate and with a sparse to moderately dense vestiture of yellow, tan, or pale dusty pink elongate setae; beak in male curved and longer than prothorax, curvature abrupt distad of antennal insertion, trisulcate laterally between base and antennal insertion, lower sulcus distinct, the median and upper ones sometimes evanescent basally, especially the median one, dorsal aspect broadly carinate from base to position of antennal insertion, area distad of carina densely punctate; beak in female curved (Fig. 101) and with a lateral sulcus above the antennal groove, the usual median and upper sulci obsolete, the upper one represented by a row of fine punctures, dorsal surface not carinate but with fine sparse punctures which are scattered over the surface distad of antennal insertion but arranged laterally towards the base so that a median non-punctate area remains; with a very sparse vestiture of pale fine setae; setae lacking in female except near margin of eye; antennae

with second funicular segment longer than first and subequal to or longer than third and fourth segments combined.

*Prothorax:* Sides usually rounded, sometimes subparallel to near apex, then constricted; with dense, coarse, reticulate punctures, frequently confluent; with a prominent longitudinal median, frequently tortuose, carina from base to apex, sometimes short of base; each puncture with a suberect or erect seta; color of setae varying from pale brown and tan to pale gray and white.

*Elytra:* One-fourth to one-third longer than wide; sides subparallel for approximately one-half, then gradually converging to apex; humeri rounded but not prominent; basal border feebly emarginate mesad of humeri; intervals 3, 5, 7, and 9 feebly to moderately costate; costae complete, those of intervals 7 and 9 frequently evanescent posteriorly; serial punctures deep and closely set; with a sparse to moderately dense vestiture of brown, tannish, yellow, and white, elongate and tapering, recumbent setae; white and lighter-colored setae forming a usually faint narrow postmedian band, and frequently scattered over the surface in small aggregates; light tan and yellowish to whitish setae condensed at base of interval 3 to form a small patch and at base of intervals 6 and 7 to form a usually conspicuous oblique patch across humerus; elytra frequently glabrous in spots, so that general appearance of vestiture is mottled; intervals sparsely set with rows of chiefly pale tan and also white, blunt-tipped, suberect setae.

*Ventral surface:* Mesosternum emarginate anteriorly. Abdominal sterna densely and coarsely punctate; fifth sternum without tubercles, usually depressed medianly and laterally; each puncture with a pale tan or white subrecumbent to suberect seta, sometimes giving the venter a "bristly" appearance.

*Legs:* Pro- and metafemoral tooth distinct, that of mesofemur frequently feeble or obsolete; sparse to moderately dense vestiture of tan to white, elongate and tapering setae.

*Male genitalia:* (Figs. 99 and 103). Aedeagus twice as long as wide and twice as long as aedeagal struts; sides converging on apical third to form an acute process; dorsal membrane V-shaped apically, variable in its basal extent, sometimes almost obliterated by lateral plates; transfer apparatus a complex of bars, with the elongate lateral pair most evident and protruding into the prephallotremic area; laterally, apical process usually not hooked, sometimes similar in shape to that of *posticatus* Boh. (Fig. 87). Length 1.00-1.05 mm., width at base .475-.500 mm., aedeagal struts .435-.475 mm.

*Type locality:* Austin, Texas.

**Type:** Male, United States National Museum Type No. 37425, T. L. Casey Collection (USNM).

**Distribution:** Records below indicate a probable range from New Jersey west to Missouri, south to Georgia, and southwest to Texas. Records from: Georgia, Missouri, New Jersey, North Carolina, eastern Texas, and Virginia.

**Biology:** The only available biological data on this species are a few specimen labels: "bred from *Quercus velutina*, issued Sept. 10, 1906" (Boerne, Texas); "bred from *Quercus nigra* acorn" (Victoria, Texas, J. D. Mitchell); "in acorns, *Quercus velutina*, issued May, 1906" (Boerne, Texas, G. A. Schattenberg); "in molasses trap" (S. W. Mt. Albermarle Co., Virginia, 1000 ft. J. M. Valentine). These records show that *carinifer* Csy. breeds in the acorns of black oak and black jack oak. Its life history is probably similar to that of the other acorn curculios, *naso* Lec. and *posticatus* Boh.

**Remarks:** The affinities of the *C. carinifer* Csy. are considered on page 104. From the description of *C. lucanus* Horn (1895), there is a possibility that it is a synonym of *carinifer* Csy. Horn's description agrees with that of *carinifer* Csy., except in the statement that the serial punctures of the elytra are not densely placed. Until the type is checked, however, no definite conclusion can be made.

Casey (1892) gives the length of the type specimen as 4.30 mm., but a measurement of the specimen reveals it to be 4.75 mm.

#### *Conotrachelus posticatus* Boheman

*Conotrachelus posticatus* Boheman, 1837, Schönh. Gen. Spec. Curc., IV, pt. 1, p. 406; (Say), 1831, Desc. N. A. Curc. New Harmony, Indiana, p. 19, *n.n.*; in Writings of Thomas Say, ed. Leconte, 1859, p. 285, *n.n.*; Leconte and Horn, 1876, Rhynchophora N. A., Proc. Amer. Philos. Soc., XV, No. 96, p. 232; Provancher, 1877, Faune Ent. Can., I, Col. p. 529; Champion, 1904, Biol. Cent. Amer., IV, pt. 4, p. 403; Blatchley and Leng, 1916, Rhynchophora N. E. Amer., p. 477; Mutchler and Weiss, 1925, Conotr. N. J., Circ. 87, Bur. Stat. and Insp., Dept. Agr., N. J., p. 21.

**Length:** 4.25-5.00 mm.

**Special characters:** Prothorax with dense but not deep punctures, the punctures never with distinct sides; beak in both sexes trisulcate laterally, metafemoral tooth distinct, prounci of male usually long and extremely acute.

**Color:** Elytra dark reddish-brown with black splotches, black sometimes predominant; prothorax usually darker than elytra.

**Head:** Densely punctate and with a sparse to moderately dense covering of pale tan or pinkish (sometimes orange) tapering setae; beak

feebly curved and longer than prothorax, curvature usually more abrupt apically; beak equal in length in both sexes; strongly trisulcate laterally between base and antennal insertion; median sulcus sometimes evanescent basally; lower sulcus possibly subdivided; dorsal surface with a distinct to broadly-rounded carina from base to distad of middle, sometimes feeble in female; dorsal surface distad of antennal insertion in male with dense elongate punctures which form small sulci; in female punctures quite dense along the lateral areas but sparse in median area; sulci sparsely set with elongate, pale tan and white setae; antennae in both sexes inserted approximately one-fourth from apex; first and second funicular segments subequal in length or the second longer than the first, each longer than any of the succeeding segments; segments six and seven globose, sides rounded.

*Prothorax*: Sides usually distinctly rounded with a constriction just before apex, sometimes subparallel behind apical constriction; dense punctures frequently confluent; disc with a usually fine, median, longitudinal carina from base to apex, sometimes evanescent sub-basally; sparsely covered with pale tan, reddish-yellow, brownish, pale white, or white elongate (some tapering) recumbent to subrecumbent setae; color of setae varying greatly; frequently a few, sometimes many, setae erect.

*Elytra*: Approximately one-fourth longer than wide; sides subparallel for over half, then converging to the apex; basal border only feebly emarginate before the humeri, which are obliquely rounded and not prominent; intervals 3, 5, 7, and 9 feebly and acutely costate, costae sometimes quite distinct, costa of interval 3 frequently flattening out on apical declivity; males usually with intervals 1 and 2 as distinctly or more costate than intervals 3, 5, 7, and 9; costae extending from base to apical declivity, that of interval 2 sometimes evanescent sub-basally or feebly interrupted in places, these costae rarely absent; females with interval 1 frequently costate and sometimes with interval 2 feebly and irregularly costate; costa of interval 2 never as distinct in female as in male; serial punctures large, closely-set, and quadrate; elytra with a sparse covering of reddish-yellow, pale tan, and white elongate and tapering recumbent setae; white setae condensed in a few scattered patches, but chiefly in a narrow, posteriorly curved, postmedian band, the distinctness of which is variable; sometimes also forming a conspicuous spot at base of third interval, sometimes absent; the other colored setae scattered over surface; sometimes the lighter ones are aggregated in patches here and there; elytra sometimes bare in spots, the vestiture then giving them a mottled appearance; each interval with a usually conspicuous row of pale tan, amber, or white, blunt-tipped, suberect setae.

*Ventral surface:* Mesosternum usually with a distinct emargination anteriorly. Abdominal sterna densely and coarsely punctate; fifth sternum sometimes finer and more densely punctate than preceding sterna, without tubercles and with or without a median depression; sparse vestiture of tan, amber, and reddish-yellow, recumbent and sub-erect setae, the latter sometimes giving the venter a "bristly" appearance.

*Legs:* Mesofemoral tooth occasionally obsolete; sparse to moderately dense vestiture of reddish-yellow, light tan, grayish, and white elongate and tapering setae.

*Male genitalia:* (Figs. 60 and 87). Aedeagus twice as long as wide and twice as long as aedeagal struts; sides gradually converging on apical third to form at apex a distinct acute process; basal portion of inner curvature not as distinct as it is apically; dorsal membrane V-shaped apically; transfer apparatus consisting of a complex of bars similar to that of *naso* Lec., the elongate lateral pair most evident and protruding into prephallotremic area; laterally, apical process hooked. Length .875-.937 mm., width at base .413-.449 mm., aedeagal struts .375-.399 mm.

*Type locality:* Florida.

*Type:* Boheman Collection, Stockholm Museum, Stockholm, Sweden.

*Distribution:* "Ranges from Ontario and New England to Wisconsin and Iowa, south to Florida," Blatchley and Leng (1916). Champion (1904, p. 404) recorded it from Mexico, Guatemala, and Panama, but stated that Central American examples were slightly different from those of the United States. Range extended to Texas. Records from: Alabama, District of Columbia, Florida, Georgia, Illinois, Indiana, Iowa, Kansas, Louisiana, Maryland, Massachusetts, Michigan, Mississippi, Missouri, New Hampshire, New Jersey, North Carolina, New York, Ohio, Oklahoma, Ontario, Pennsylvania, Rhode Island, South Carolina, Tennessee, Texas, Virginia, and West Virginia.

*Biology:* Literature records of this species are scarce, and those available are not in agreement. Hamilton (1895) records *posticatus* Boh. as commonly bred from the fruits of *Crataegus*, while Pierce (1907a), quoting E. A. Schwarz, states that the larvae dwell in galls of certain *Phylloxera* on hickory leaves, the *Phylloxera* probably perishing from starvation. Pierce (1907b) reports breeding this species from prematurely fallen hickory nuts collected on June 8 at Logansport, La. He states, "The larvae clean out practically the entire nut and then enter the ground for pupation." Brooks (1910) reared *posticatus* Boh. from chestnut oak acorns, and in his report quotes Webster as breeding it from white oak acorns. Blatchley and Leng (1916) record beating this species from the blossoms of wild plum, while Wellhouse (1922) lists its hosts as *Crataegus*, *Prunus*, and *Carya*.

The specimen records are as follows: "in *Q. alba*" (Colmanville, Pa., F. C. Pratt); "*Q. pedunculata* and *Q. rubra*" (District of Columbia); "*Q. durandii*" (Victoria, Texas, J. D. Mitchell); "in open chestnut bur" (Framingham, Mass., C. A. Frost); "hibernating beneath leaves of *Q. alba*, *coccinea*, *palustris*, *velutina*, and *borealis* var. *maxima*" (Wortendyke, N. J., H. F. Schoof).

The majority of the records indicate that *posticatus* Boh. probably breeds in acorns of various species of *Quercus*. Whether hickory nuts and Phylloxera galls also serve as hosts cannot be definitely determined. The record from Phylloxera galls on hickory appears more like the work of *elegans* (Say), while that from hickory nuts could well apply to *affinis* Boh. As both of these species belong to Group I (the two-toothed femur group), it does not seem likely that the specimens from which these records were taken were misidentified. Nevertheless, it would appear that until corroborative data are obtained, the records from hickory nuts and Phylloxera galls should be considered questionable. Hamilton's (1895) record of *Crataegus* as a host likewise is questionable.

Brooks (1910) states that the life-history of *posticatus* Boh. at French Creek, West Virginia, is similar to that of *naso*, Lec. On this basis the larva is the overwintering stage, with the adult appearing in June, July, and August. The writer, however, has found adults of this species hibernating beneath oak leaves on December 26 to 29 in New Jersey, which indicates a somewhat different life cycle than that reported by Brooks (1910). From the biological data available, it appears that there is need for a more careful study of the life history and host plants of this species.

Specimen records show that *posticatus* Boh. has been attracted to light traps and in one instance to a molasses trap.

*Remarks:* The relationships of this species have been briefly mentioned under *C. naso* Lec. Champion (1904) mentions a variety having the first and second intervals costate, but this is more a sex character of the males.

#### *Conotrachelus recessus* (Casey)

*Loceptes recessus* Casey, 1910, Can. Ent., 42, p. 130.

*Conotrachelus atokanus* Fall, 1913, Trans. Amer. Ent. Soc., 39, p. 65.

*Length:* 2.5-3.0 mm.

*Special characters:* First funicular segment of antenna subequal in length to the next two combined.

*Color:* Elytra chiefly reddish-brown with a little black; prothorax piceous.

*Head:* Densely punctate and thickly covered with broad, light tan,

recumbent scales, truncate at the tip; a few pale elongate setae also present; beak feebly curved, but distinctly straight in female below antennal insertion; subequal in length to prothorax and slightly longer in female; feebly sulcate laterally; lower sulcus distinct; median sulcus evanescent basally; upper sulcus replaced by punctures; dorsal surface non-carinate; distad of antennal insertion with dense elongate punctures in male; punctuation finer and indistinct in female; vestiture of truncate-tipped scales and elongate setae, light tan setae denser basally; antennae inserted approximately one-third from apex in male, one-half in female.

*Prothorax:* Sides either subparallel or feebly rounded from base to near apex, then constricted; disc with dense, medium-sized, shallow punctures; non-carinate and without tubercles; densely clothed with a mixture of broad, truncate-tipped, recumbent, tan and white scales, the tan scales predominant, the white ones along the sides condensed in small spots at the basal angles; elongate, recurved, brown, tan, and white setae sparsely interspersed among scales, vestiture usually obscuring punctuation.

*Elytra:* One-third longer than wide; sides subparallel for about two-thirds, then gradually converging to the apex; basal border feebly emarginate mesad of humeri; the latter not prominent, rounded; intervals 3, 5, and 7 feebly convex but not costate; serial punctures small, obscured by the vestiture; dense vestiture of oblong tan (golden) and white scales, the golden scales greatly predominant, the white scales aggregated basally at the humeri and the third intervals and sparsely scattered medially at the apical declivity and between the middle and the base; each interval with a row of elongate, recurved, pale, white, and dark brown setae which are most abundant and evident on convex intervals, especially basally.

*Ventral surface:* Mesosternum not protuberant, sloping anteriorly. Abdominal sterna coarsely and densely punctate; punctures of sterna 1 and 2 larger than those of the succeeding sterna; sternum 5 without tubercles or depressions; each puncture with a light tan or white seta; setae along the sides broader and forming patches.

*Legs:* Femoral tooth distinct; unci not dentate in either sex, in male tapering and usually acute, in female stubby and bluntly rounded at apex; legs with a moderately dense vestiture of recumbent tan and white setae; femora with a few pale scales mixed among the apical setae.

*Male genitalia:* (Figs. 63 and 90). Aedeagus elongate, three times as long as wide at base and four times the length of the aedeagal struts; sides bisinuate; apex without a process; dorsal membrane narrowed for approximately the median half and then expanded both basally and apically; apical border broadly curved; dorsal area possibly sclerotized;

transfer apparatus protruding into prephallotremic area. Length .500 mm., width at base .165 mm., aedeagal struts .125 mm.

*Type locality:* Atoka, Oklahoma.

*Type:* Male, Wickham, T. L. Casey Collection (USNM).

*Type:* Male, *atokanus* Fall: Museum of Comparative Zoology Type No. 25228, Atoka, Indian Territory, June 13-15, Wickham (MCZ).

*Distribution:* Ranges from Iowa to Oklahoma, Arkansas, and Texas. Records from: Arkansas, Iowa, Kansas, Oklahoma, and eastern Texas.

*Biology:* Five specimen records, each indicating a different host plant, furnish the only biological data available for *recessus* (Csy.): "peaches" (Bonham, Texas, E. and G. Wheeler); "*Quercus minor*" (Clarksville, Texas, E. S. Tucker); "box elder" (Dallas, Texas, W. D. Pierce); "on *A. cannabinum* L. var. *pubescens*" (W. E. Hoffman); and "on *Maclura pomifera* (Osage Orange)" (Dallas, Texas, W. D. Pierce).

This species has also been collected "at lights" in Fayetteville, Arkansas.

*Remarks:* This small species was originally described by Casey (1910) who placed it in the Tychiini as the type of the monobasic genus *Loceptes*. Fall (1913) correctly described the same species as *Conotrachelus atokanus*, and it was known under this name until Buchanan (1937) published the synonymy.

*C. recessus* (Csy.), by its small size, golden-colored scales, and recurved elytral setae, can be readily distinguished from other species of *Conotrachelus*.

#### *Conotrachelus geminatus* Leconte

*Conotrachelus geminatus* Leconte, 1876, Rhynchophora N. A., Proc. Amer. Philos. Soc., XV, No. 96, p. 232; Dejean, 1837, Cat. Col., Paris, p. 322, *n.n.*; Blatchley and Leng, 1916, Rhynchophora N. E. Amer., p. 478; Mutchler and Weiss, 1925, Conotr. N. J., Circ. 87, Bur. Stat. and Insp., Dept. Agr., N. J., p. 21.

*Length:* 3.85-4.85 mm.

*Special characters:* Setae of median portion of abdominal sterna 2 to 5 short, scarcely visible; femoral tooth not acute and usually feeble.

*Color:* Elytra reddish and prominently splotted with black; black sometimes predominant.

*Head:* Densely punctate; a short pale seta arising from each puncture; beak stout, curved either feebly or distinctly, curvature sometimes more abrupt apically; subequal in length to prothorax and in both sexes; occasionally trisulcate laterally between base and antennal insertion; upper or median sulcus, or both, however, frequently feeble and obscure; lower sulcus always distinct; sulci, when absent, replaced by dense punc-

tures, which give the area a distinctly roughened appearance; dorsal surface occasionally carinate to near or distad of middle, but usually non-carinate; apical tip distad of antennal insertion with fine, elongate punctures dorsally; punctures moderately dense to dense, usually sparse in the female, and sometimes obscure; lateral area proximad of antennal insertion sparsely set with pale tan setae; antennae inserted one-fourth to one-third before apex; first two funicular segments subequal in length and each longer than any of the others.

*Prothorax*: Sides subparallel or parallel to just before apex, then sharply constricted; sometimes gradually rounded from base to apex, outline sometimes varying in form on different sides in the same specimen; with dense coarse reticulate punctures, deep and usually not confluent, but occasionally a few confluent apically; non-carinate and without tubercles; each puncture with a suberect pale tan or amber seta; sometimes a tiny patch of white oblong subrecumbent setae on the lateral median border of the disc.

*Elytra*: Approximately one-third longer than wide; sides subparallel for over half, then sharply converging to the apex; basal border emarginate before the humeri; the latter varying in prominence, obliquely rounded; intervals 3 and 5 sometimes convex but not costate, at the most with feeble, broad elevations apically; intervals 7 and 9 sometimes feebly to moderately costate, especially basally; serial punctures coarse; very sparse vestiture of tan, pale tan, silvery, and white recumbent setae, the white setae aggregated into small scattered patches among the predominantly tan and pale tan setae which, plus the variegated color markings of the elytra, give the wing covers a very mottled appearance; or more abundant apically along intervals 3 and 5; above setal arrangement variable; occasionally pale white setae predominate; numerous areas bare; intervals set with rows of suberect pale and dark tan setae, usually distinct but sometimes scarcely noticeable.

*Ventral surface*: Mesosternum not protuberant, with a slight slope basally. Abdominal sterna moderately to coarsely punctate; sternum 1 usually less densely and more coarsely punctate than 2; sternum 5 usually more densely punctate than 2, 3, and 4; punctures of sterna 3 and 4 sometimes fine and sparse; punctation of all sterna varies greatly in density, so that digressions from above pattern are frequent; sternum 5 without tubercles, with a distinct median depression in the female, at most feebly depressed in male; each puncture with a short, scarcely visible, pale amber seta, these setae occasionally replaced by longer white or tan setae, particularly on sternum 1 and laterally on 2, 3, and 4.

*Legs*: Metaunci not dentate in either sex; legs sparsely clothed with pale tan, tan, and white setae.

**Male genitalia:** (Figs. 61 and 88). Aedeagus twice as long as wide at base, and two to two and one-half times as long as aedeagal struts; outer curvature bisinuate; basal portion of inner curvature difficult to detect; apex with a broad, blunt process; dorsal membrane very small, V-shaped apically, but edge difficult to detect; transfer apparatus consisting of a pair of semicircular bars; laterally, aedeagus highly arched, dorsal and ventral curvatures gradually approaching apically. Length .812-.875 mm., width at base .336-.399 mm., aedeagal struts .262-.375 mm.

**Type locality:** Leconte (1876) at the time of his description of *geminatus* had before him specimens from Illinois, Kansas, and Maryland. Of the two specimens now in the Leconte Collection, one bears a pink disc indicating Leconte's symbol for "Middle States," the other a green disc, probably referring to Nebraska. The author has interpreted Leconte's term "Middle States" as including Maryland, thereby making this specimen available as a lectotype.

**Lectotype,** hereby designated: The specimen labelled "*geminatus* + Dej." and bearing a pink disc in the J. L. Leconte Collection (MCZ).

**Distribution:** "Ranges from Quebec and New England to Iowa and Kansas, south to Florida," Blatchley and Leng (1916). Range extended west to Nebraska. Records from: District of Columbia, Illinois, Indiana, Iowa, Kentucky, Maryland, Massachusetts, Michigan, Missouri, Nebraska, New Jersey, New York, North Carolina, Ohio, Pennsylvania, and Virginia.

**Biology:** Specimen records show that *C. geminatus* Lec. has been bred from the flower heads of *Bidens* (beggar-tick) at Rosslyn, Virginia, by A. N. Caudell, and from the fertile flowers of the giant ragweed at Kinderhook, Illinois, by L. Hack. Pierce (1907a) records the species on *Ambrosia trifida*. These are the only definite host records for this species.

Other specimen data are: "*Carex frankii*" (W. Point, Indiana) and "trap lantern" (Lafayette, Indiana).

**Remarks:** Leconte (1876) and Blatchley and Leng (1916) considered Dejean (1837) as the author of the name *geminatus* but Dejean's *geminatus* is a *nomen nudum*. Therefore, Leconte (1876), being the first to describe the species, is the author of the species. Mutchler and Weiss (1925) and Hustache (1936) correctly designated the species *geminatus* Lec.

Leconte (1876) and Hustache (1936) both list *C. puncticollis* Walsh as a synonym of *geminatus* Lec., but this species from its description appears to be a synonym of *cribricollis* (Say) rather than *geminatus* Lec. A discussion of this synonymy is given under *cribricollis* (Say) on page 117.

*Conotrachelus cribricollis* (Say)

*Cryptorhynchus cribricollis* Say, 1831, Desc. N. A. Curc., New Harmony, Indiana, p. 28, in Writings of Thomas Say, ed. Leconte, 1859, p. 296.

*Conotrachelus cribricollis* (Say) Boheman, 1837, Schönh. Gen. Spec. Curc., IV, pt. 1, p. 446; Leconte and Horn, 1876, Rhynchophora N. A., Proc. Amer. Philos. Soc., XV, No. 96, p. 233; Blatchley and Leng, 1916, Rhynchophora N. E. Amer., p. 479; Mutchler and Weiss, 1925, Conotr. N. J., Circ. 87, Bur. Stat. and Insp., Dept. Agr., N. J., p. 21.

*Conotrachelus puncticollis* Walsh, 1864, Proc. Bost. Soc. Nat. Hist., IX, p. 310, preoccupied by *puncticollis* Fahreus, 1837, Schönh. Gen. Spec. Curc. IV, pt. 1, p. 405 (see Col. Cat., Junk and Schenkling, Pars 151, 1936, p. 26) (new synonymy).

*Length:* 3.80-4.85 mm.

*Special characters:* Undersurface of apical portion of beak (viewed laterally) with prominent, usually long, suberect and erect amber setae; elytra with a "bristly" appearance; many setae of median portion of abdominal sterna 2 to 5 long and conspicuous; femoral tooth prominent and acute, usually a minute denticle distad of tooth.

*Color:* Prothorax and elytra piceous to black.

*Head:* Densely punctate; with a sparse to moderately dense covering of tan and white recumbent setae; beak stout, curved, usually abruptly bent apically near antennal insertion; shorter than prothorax, equal in length in both sexes; distinctly trisulcate laterally between base and antennal insertion; dorsal and median sulci often replaced basally by dense punctures; median sulcus distinct and broad apically; dorsal surface finely and acutely carinate from base to distad of middle; surface distad of antennae with coarse, elongate punctures, moderately dense to dense; sparse to moderately dense vestiture of tan and white setae which are denser basally; antennae inserted approximately one-fourth to one-third before tip; first two funicular segments subequal in length and each longer than any of the other segments.

*Prothorax:* Feebly rounded from base to apex or subparallel to one-fourth before apex, then constricted; very coarsely and deeply punctured (foveate); no areas between punctures other than their walls; depth of discal punctures approximately one-fourth to one-half their diameters; punctures frequently confluent, forming longitudinal ridges; each puncture with a prominent brown or tan erect seta.

*Elytra:* Approximately one-third longer than wide; sides subparallel for more than half, then gradually converging to the apex; basal border not or but feebly emarginate before humeri; the latter not prominent and obliquely rounded; intervals feebly convex but not costate, more convex apically; serial punctures large, deep, quadrate, and closely set; with a moderately dense, variegated vestiture of light tan, brownish, and white recumbent setae; the white setae in scattered patches over the surface,

and condensed with light tan setae on the humeri and at base of interval 3; each interval set with a prominent row of long, suberect, tan, brown, and white setae which give the elytra a "bristly" appearance.

*Ventral surface:* Mesosternum not protuberant, or only slightly so. Abdominal sterna with large, deep, dense, reticulate punctures; fifth sternum without tubercles or depressions; each puncture with a subrecumbent or suberect pale tan or amber seta; suberect setae conspicuous and much longer than subrecumbent ones; a few lateral subrecumbent setae white.

*Legs:* Metaunci in male short and blunt at apex, in female acute; legs with a sparse vestiture of tan, brown, and white recumbent to suberect setae, the latter chiefly on the tibiae.

*Male genitalia:* (Figs. 62 and 89). Aedeagus approximately twice as long as wide at base and twice as long as aedeagal struts; sides bisinuate sometimes feebly so, and widened to obtuse points at the apex; the latter broad and with a feeble rounded process; dorsal membrane small, sometimes extending farther basally than in Fig. 62; apical border broadly U-shaped; transfer apparatus consisting of a pair of prominent dorsal semicircular bars and two lateral pairs, the latter with one bar above the other. Length .687-.738 mm., width at base .336-.363 mm., aedeagal struts .274-.336 mm.

*Neotype locality:* Urbana, Illinois. Say's type locality: Mississippi.

*Neotype:* Male, June 14, 1940, H. B. Petty, light trap (HFS).

*Neallotype:* Female, Havana, Illinois; June 20, 1928; T.H.F. and H.H.R. (ISNHS).

*Neoparatypes:* ALABAMA: Mobile Co., H. P. Loding, 2 ♂, (USNM); Mobile, April 18, 1910, on *Pinus palustris*, W. D. Pierce, ♀, (USNM); ILLINOIS: Urbana, April 7, 1889, Ac. No. 25014, C. A. Hart, ♂, (ISNHS); Galesburg, ♂, (ISNHS); Dubois, Ac. No. 16058, A. A. Hinkley, ♂, (ISNHS); Golconda, May 30, 1928, at light, T. H. Frison, 2 ♀, (ISNHS); Pegrim, May 27, 1903, Ac. No. 34389, Titus, ♀, (ISNHS); Grand Tower, June 2, 1913, in woods at night, ♀, (ISNHS); Urbana, April 15, 1939, hibernating at edge Brownfield Woods, H. F. Schoof, 2 ♀, (HFS); IOWA: Lee County, July 6, 1925, Rockenbach, ♀, (WPH); Ames, July 13, D. Stoner, ♂, (USNM); KANSAS: Topeka, March 15, ♂, (USNM); KENTUCKY: Lexington, November 24, 1894, No. 1912, ♀, (HFS); LOUISIANA: Bayou Sara, January 24, 1879, ♂, (USNM); MARYLAND: Plum Point, May 28, 1922, L. L. Buchanan, ♀, (USNM); MISSISSIPPI: Jackson, April 6, 1912, A. A. Green, S. 3308, ♂, ♀, (HFS); Cleveland, May 24, 1915, J. S. Wakefield, S. 4024, 2 ♀, (USNM); Jackson, Oct. 1906, W. M. Bamberger, ♀, (USNM); West

Point, August 12, H. S. Barber, ♀, (USNM); West Mississippi, July 27, 1912, J. M. Johnson, ♀, (USNM); Scooba, S. 3643, R. Stuart, ♀, (USNM); Skene, April 24, 1911, G. Janoush, S. 3053, ♀, (USNM); MISSOURI: Columbia, July 14, 1905, ♀, (U Mo); Columbia, August 29, 1924, E. T. Jones, ♀, (HFS); NORTH CAROLINA: Southern Pines, January 6, 1909, A. H. Manee, Nason Collection, ♀, (UIDE); Garner, December 4, 1940, hibernating in hedgerow, ♀, W. A. Majure, (HFS); PENNSYLVANIA: Allegheny Co., ♀, (USNM); SOUTH CAROLINA: Clemson College, May 9, 1930, D. Dunavan, ♀, (USNM); TENNESSEE: Memphis, March 12, 1893, H. Soltau, ♀, (USNM); TEXAS: Devil's River, June 5, 1907, E. A. Schwarz, ♀, (USNM), Devil's River, May 6, 1907, at light, Bishopp and Pratt, ♂, (HFS), ♂, (USNM); VIRGINIA: ♂, (USNM).

*Distribution:* "Ranges from New England to Northern Illinois, south to Louisiana and Texas," Blatchley and Leng (1916). Range extended west to Kansas and Nebraska and southeast to Alabama and Florida. Records from: Alabama, Arkansas, Florida, Illinois, Indiana, Iowa, Kansas, Kentucky, Louisiana, Maryland, Missouri, Mississippi, Nebraska, North Carolina, Ohio, Pennsylvania, South Carolina, Tennessee, Texas and Virginia.

*Biology:* Other than the following few specimen records there is no biological information available on this species. "On *Pinus palustris*" (Mobile, La., W. D. Pierce); "on Ambrosia" (Central Mo., C. V. Riley); "in cotton fields" (Paris, Texas, F. C. Bishopp); "on cotton" (Valdosta, Ga., W. L. Lowry); "jarred from peach" (Fort Valley, Ga., O. I. Snapp); "hibernating under leaves at edge of woods" (Urbana, Ill., H. F. Schoof); "hibernating under pokeweed, blackberry, aster, and other weeds" (Garner, N. C., W. A. Majure); "collected in weeds, trash" (Florence, S. C., C. F. Rainwater); and "at light" (Devil's River, Texas, Bishopp and Pratt, and Riley County, Kansas, P. J. Parrot).

*Remarks:* This species, in contrast to *retentus* (Say) and *elegans* (Say), has not been the source of much confusion. It is easily distinguished from other species of *Conotrachelus* by its widely and deeply punctate (foveate) prothorax and by the numerous suberect setae which give the elytra a "bristly" appearance. The chief difficulty encountered with the identification of *cribricollis* (Say) arises from the usual occurrence of a minute denticle distad of the femoral tooth. According to the grouping of this genus, this species should belong to Group I which is characterized by having two femoral teeth. However, *cribricollis* (Say) bears little affinity to any of the species in that group excepting possibly *nivosus* Lec. which, as previously mentioned, is also unrelated to most of the species included therein. Just what the relationships of these two

"misfits" are, cannot be stated at this time. With the material on hand the only congruous statement that can be made is that both species appear to be intergrades between Groups I and II. *C. cribricollis* (Say) has been placed in the one-toothed group because the denticle is sometimes absent and because when it is present the specimen is usually considered one-toothed, since the denticle is often so minute that it is overlooked.

*C. puncticollis* Walsh (1864) is listed here as a synonym of *cribricollis* (Say), although it has been considered by Leconte (1876), Leng (1920), and Hustache (1936) as a synonym of *geminatus* Lec. As the type specimen of *puncticollis* Walsh (1864) has apparently been lost, this synonymy has been based entirely on Walsh's original description which is given below:

*"Conotrachelus puncticollis*, n. sp.—Head black with a coppery lustre, finely pubescent, with very fine confluent punctures; rostrum suddenly bent inwards at two-thirds the distance to its tip, as in *C. anaglypticus* Say. Thorax black, sparsely pubescent, much narrower than the elytra, as wide as long, scarcely contracted at its base, but much contracted at its tips, with very large deep punctures confluent above, so as to form towards its tips three or four irregular longitudinal carinae. Elytra regularly punctate-striate, without any carinae, the striae shallow and wide, the punctures moderate; the interstices flattish, very finely punctured, and with a row of short cinereous bristles upon each directed backward; the whole elytram irregularly mottled with whitish and brown, so as to appear gray, with 3 or 4 indistinct brown fasciae, except on the base of the third interstice, where there is a conspicuous short, whitish vitta. Legs blackish with fine short whitish pubescence, the second tooth of the femora obsolete. Length  $\frac{3}{20}$ th inch. One specimen. Near *C. cribricollis*, Say, but that species has the elytra black without any bristles. Except in the comparative shortness of the thorax, it resembles in its shape *C. anaglypticus*, Say, and is much broader than *C. nenuphar* the 'curculio.'"

In this description it will be noted that the thorax (prothorax) is characterized as having very large, deep punctures which are confluent above, so as to form towards its tip three or four longitudinal carinae. This character is similar to that found in *cribricollis* (Say), but differs from that of *geminatus* Lec. where the prothoracic punctures never form longitudinal ridges. The remainder of the description can be applied equally well to both *cribricollis* (Say) and *geminatus* Lec. The beak in *cribricollis* (Say) usually is abruptly bent at the apical third, but *geminatus* Lec. sometimes also has the beak similarly shaped apically. Because the description of the prothoracic punctuation of *puncticollis* Walsh fits *cribricollis* (Say) and not *geminatus* Lec., the first two of these names are here considered synonyms.

As will be noted, Walsh states in his description that *cribricollis* (Say) does not have elytral bristles. This statement is confusing, since *cribricollis* (Say) definitely does have erect elytral setae (bristles). At that time (1864), the only available description of *cribricollis* was the one published by Say (1831) which stated that the body had numerous very short hairs, but did not mention whether or not the hairs were erect. Say described the prothorax as having the whole surface covered by large concave punctures, without any very flat space between them, so that it is concluded that he had before him the species which has been interpreted as *cribricollis* (Say) by Leconte (1876), Blatchley and Leng (1916), and others, as well as by the present writer. Just which species Walsh was referring to as *cribricollis* (Say) is not at all clear. Possibly the erect bristles had been rubbed off in the specimen of *cribricollis* (Say) that Walsh had before him.

*C. puncticollis* dates from Walsh in 1864 and not 1863. As with *C. crataegi* Walsh, the original description of the species was published in the Proceedings of the Boston Society of Natural History for the year 1863, but the actual date of publication was March, 1864 (*loc. cit.*, bottom of page 305). Walsh's description was also published in *Prairie Farmer*, n. s., Vol. 12, No. 2, July 11, 1863, p. 21; but as this agricultural journal is not a technical publication, this earlier description is invalid.

### GROUP III

This group corresponds to Group II of Leconte and Horn (1876) and to Group IV of Blatchley and Leng (1910). It consists of five species. Three of them, *tuberosus* Lec., *anaglypticus* (Say), and *leucophaeatus* Fahr., occur in the midwestern region. The other two species, *obesulus* Hust. and *coronatus* Lec., are rare and have been found only in the southeastern states. All species agree in having the prothorax with a dorsal, median, longitudinal furrow, thus being readily separated from other species of *Conotrachelus*. In addition, the species in this area have the beak subequal to or shorter than the prothorax; first funicular segment of antennae subequal to or longer than second, each longer than any succeeding segment; prothorax densely and usually coarsely punctate, clothed laterally with two lines of white or tannish vestiture; elytral intervals 3, 5, 7, and 9 costate; costa of interval 5 always interrupted subbasally; elytral vestiture chiefly of recumbent setae; mesoscutellum from lateral aspect abruptly declivent basally; metasternum in male never grooved from meso- to metacoxa; abdomen coarsely punctate; femora with a tooth and usually a small denticle; aedeagus elongate with a dorsal membrane and an apical process; transfer apparatus a complex of sclerotized bars.

Group III is known as the "*anaglypticus* group," and this designation in contrast to those of Groups I and II typifies the group, all species being quite similar in habitus and closely related.

#### KEY TO SPECIES OF GROUP III

1. Costa of interval 3 strongly interrupted twice (anterior interruption occasionally feeble) to form three elevations, the median and posterior ones abrupt and prominent; aedeagus with apical process pointed (Fig. 66), length 2.5-3.0 mm.....*tuberosus* Leconte, p. 119
- 1- Costa of interval 3 sometimes feebly interrupted anteriorly, rarely interrupted twice; if so, elevations formed are not prominent, and specimens are 4.0-5.5 mm. with elytral vestiture conspicuously white; aedeagus with apical process rounded (Figs. 67 and 68)..... 2
2. Elytral vestiture usually not conspicuously white; if so, the white transverse band is always behind the subbasal interruption of costa of interval 5; each elytron with an oblique bar of yellowish vestiture just behind the humerus; bar usually prominent, sometimes faint, but always evident; male metatibia deeply emarginate before uncus (Fig. 32a); aedeagus as shown in Fig. 67.....*anaglypticus* (Say), p. 121
- 2- Elytral vestiture conspicuously white, with a broad transverse white band extending from apical declivity to posterior edge of humerus; elytron never with an oblique yellowish bar behind humerus; male metatibia not emarginate before uncus; aedeagus as shown in Fig. 68.....*leucophaeatus* Fahreus, p. 126

#### *Conotrachelus tuberosus* Leconte

*Conotrachelus tuberosus* Leconte, 1876, Rhynchophora N. A., Proc. Amer. Philos. Soc., XV, No. 96, p. 233; Blatchley and Leng, 1916, Rhynchophora N. E. Amer., p. 480.

*Length:* 2.5-3.0 mm.

*Special characters:* Beak quadrisulcate laterally; eyes not contiguous beneath; interocular distance equal to or more than length of first funicular segment of antenna; median elevation of elytral interval 3 hump-like.

*Color:* Elytra and prothorax dark brown or black.

*Head:* Densely punctate, punctures larger apically; densely rugulose; bare; the punctures with fine, brown, inconspicuous setae; beak stout, feebly curved to near the antennal insertion, then abruptly bent; shorter than prothorax, equal in length in both sexes; quadrisulcate laterally between base and antennal insertion, the usual single lower sulcus definitely divided; dorsal surface distinctly carinate from base to distad of middle, usually acutely; apical tip distad of carina with moderately dense to dense elongate punctures; densely rugulose; sulci sparsely set with reddish-yellow, tan, and white setae; antennae inserted approximately one fourth from apex; first funicular segment stouter than second.

*Prothorax:* Sides slightly widening from base to approximately one-

third before apex, then constricted; densely and coarsely punctate; ridges bordering median furrow variable in distinctness; usually not carinate medianly; occasionally a feeble, median, longitudinal ridge behind median furrow; densely rugulose; each puncture with a brown, tan, or white subrecumbent or suberect seta; setae variable in length; vestiture densest and most prominent along each side where white setae are condensed to form two lines, one sinuate and extending diagonally from basal angle to postocular lobe, the other usually extending from just within basal angle apically to about the middle, these two lines united apically by an oblique line; lines of white vestiture sometimes obscure.

*Elytra*: Three-fourths to four-fifths as wide as long; sides subparallel for more than half, then abruptly converging to apex; basal border feebly emarginate before humeri; the latter not prominent and rounded; intervals 3 and 5 costate; costa of interval 3 usually strongly interrupted twice to form three hump-like elevations; median elevation longer and more prominent than either of the other two; anterior elevation and anterior interruption sometimes feeble; costa of interval 5 usually similarly interrupted, sometimes complete posteriorly; median and posterior elevations never as prominent as respective ones of interval 3, sometimes small and widely separated; interval 7 usually with a feeble costa, interrupted once basally; interval 9 usually feebly costate from before base to apex; serial punctures close-set, coarse; punctures so coarse and close that sometimes intervals almost obliterated; with a sparse vestiture of reddish-yellow, tan, and white setae; setae prominently condensed at base of interval 3, also more abundant between median and posterior elevations of interval 3.

*Ventral surface*: Mesosternum angulate on anterior border, feebly protuberant. Abdominal sterna with large, coarse, dense punctures; surface densely rugulose; sternum 5 not tuberculate or depressed; each puncture with a brown, tan, or white seta, variable in length.

*Legs*: Femora with a large conspicuous tooth; a small denticle sometimes also present; profemora only with a distinct anterior bulge opposite tooth; metaunci not dentate in either sex; femoral area distad of tooth with a moderately dense to dense vestiture of recumbent and subrecumbent white and tan setae, metafemoral vestiture denser; femoral area proximad of tooth with sparse vestiture.

*Male genitalia*: (Figs. 66 and 93). Aedeagus two and one-half times as long as wide, and two and one-half times the length of the aedeagal struts; sides slightly constricted medially and gradually converging apically to form a distinct, pointed process; dorsal membrane V-shaped apically; transfer apparatus with a pair of bars J-shaped, a second pair straight, the latter beneath and extending obliquely across the inner angle

of J-shaped bars; apparatus projecting into prephallotremic area. Length .649-.687 mm., width at base .238-.250 mm., aedeagal struts .250 mm.

*Type locality:* Illinois.

*Lectotype*, hereby designated: Museum of Comparative Zoology Type No. 5221-2, J. L. Leconte Collection (MCZ).

*Lectoparatypes:* Museum of Comparative Zoology Type No. 5221-3, Illinois, J. L. Leconte Collection (MCZ); Museum of Comparative Zoology Type No. 5221-1, no locality, J. L. Leconte Collection (MCZ).

*Distribution:* Ranges from District of Columbia to Iowa south to Louisiana. Records from: Alabama, District of Columbia, Illinois, Iowa, Indiana, Maryland, Ohio, and Virginia.

*Biology:* Ulke (1902) records *tuberosus* Lec. as occurring on *Urtica*, and Blatchley (1922) reports the same host, stating that for two summers numerous specimens of *tuberosus* Lec. were swept from nettles (*Urtica*) in dense woodlands in Marion County, Indiana. No other data are available.

*Remarks:* *C. tuberosus* Lec. resembles those species of Group I in which the elytral costae are abruptly interrupted to form distinct elevations. Its prothoracic sculpture and its male genitalia, however, clearly indicate its placement in Group III. Other than the costal interruptions of the elytra it is quite similar to *anaglypticus* (Say) of this group.

#### *Conotrachelus anaglypticus* (Say)

*Cryptorhynchus anaglypticus* Say, 1831, Desc. N. A. Curc. New Harmony, Indiana, p. 18, in Writings of Thomas Say, ed. Leconte, 1859, p. 282.

*Conotrachelus anaglypticus* (Say) Fahreus, 1837, Schönh. Gen. Spec. Curc. IV, pt. 1, p. 418; Leconte and Horn, 1876, Rhynchophora N. A., Proc. Amer. Philos. Soc., XV, No. 96, p. 234; Champion, 1904, Biol. Cent. Amer., IV, pt. 4, p. 420; Blatchley and Leng, 1916, Rhynchophora N. E. Amer., p. 480; Mutchler and Weiss, 1925, Conotr. N. J., Circ. 87, Bur. Stat. and Insp., Dept. Agr., N. J., p. 19.

*Conotrachelus rubiginosus* Boheman, 1845, Schönh. Gen. Spec. Curc. VIII, pt. 2, p. 28.

*Length:* 2.95-4.66 mm. (usually 3.7-4.3 mm.).

*Special characters:* Eyes contiguous beneath or nearly so; interocular space not greater than twice the diameter of a facet; median longitudinal furrow of prothorax usually feeble, sometimes scarcely evident; elytral costae of intervals 3, 7, and 9 usually acute and complete.

*Color:* Elytra light reddish-brown to piceous mixed with black; prothorax dark piceous to black.

*Head:* Densely punctate, rugulose, sparsely covered with recumbent brownish-yellow and white setae; beak feebly curved, curvature usually abrupt near the antennal insertion; subequal to or shorter than prothorax;

equal in length in both sexes; deeply trisulcate laterally between base and antennal insertion, median and upper sulci sometimes evanescent towards base; median sulcus sometimes with a cross-wall; lower sulcus occasionally divided; sulci punctate; dorsal surface with a distinct carina from base to distad of middle, extremely acute in male, sometimes barely extending beyond middle in female; apical tip distad of carina with dense, elongate punctures, so elongate as to form small sulci; lateral sulci sparsely set with tan, brownish-yellow, and white elongate setae; antennae inserted approximately one-third from apex in female, approximately one-fourth in male; first funicular segment stouter than second.

*Prothorax*: Subequal in length and width; sides subparallel to near apex, then narrowed; furrow sometimes narrowed apically; a conspicuous tubercle sometimes at posterior termination of each ridge bordering furrow; with dense, moderately coarse, uneven punctures; disc occasionally with a feeble median longitudinal carina extending from in front of middle to before base; carina entering basal third or fourth of median furrow, rarely prominent; two oblique, feeble to distinct, broad depressions on either side behind the middle; depressions approaching basally; when distinct, that edge proximad of base sometimes tuberculate basally; surface densely rugulose; sparse vestiture of tan, brown, and white, recumbent to suberect, frequently recurved setae; some setae much longer than others; the shorter white setae condensed into two prominent, lateral lines on each side; the lower line sinuate and extending from basal angle diagonally to postocular lobe; the upper line feebly curved, extending from inside of basal angle to before apex; lines united subapically by an oblique line; sometimes feeble additional branches also present.

*Elytra*: Approximately one-fourth longer than wide; sides subparallel for more than half, then converging to apex, or with a subbasal bulge followed by gradual convergence which is more abrupt beyond the middle; basal border feebly or not emarginate before the humeri; the latter not prominent, obliquely rounded; intervals 3, 5, 7, and 9 acutely costate; costa of interval 5 distinctly interrupted subbasally; that of 3 sometimes with a faint indication of an interruption opposite that of 5, usually complete; costae of intervals 7 and 9 occasionally feeble; that of 7 occasionally interrupted subbasally; striae marked by large coarse punctures (sometimes larger than those of prothorax); with a sparse to moderately dense vestiture of oblong white, yellow, and pale tan recumbent setae; yellowish setae usually condensed on basal half at humeri and intervals 3 and 5, and in a conspicuous oblique bar which extends from interval 7 through the subbasal interruption of costa of interval 5 to interval 3; yellow setae also in patches over elytra; white setae usually scattered over apical half and forming with the pale tan ones a

usually faint postmedian band; sometimes white setae predominate, replacing yellow setae in basal area (except in oblique bar), and forming a prominent broad postmedian band; the latter sometimes split into two or three narrow transverse bands; discal area between third intervals and apical declivity behind postmedian band with vestiture sparse; alternate intervals set with brown, tan, and white subrecumbent elongate setae, sometimes conspicuous on costate intervals where they are directed toward crest of costa.

*Ventral surface:* Mesosternum angulate anteriorly, protuberant; metasternum usually with a ridge from mesocoxa to metacoxa. Abdominal sterna 1, 2, and 5 with sparse to dense, deep punctures; sterna 3 and 4 usually less densely punctate than 1, 2, and 5; the latter sometimes with finer and denser punctures than sterna 1 and 2; relative denseness and coarseness of punctures varying greatly between 1, 2, and 5; surface densely rugulose; each puncture with a fine brown or amber seta; lateral setae broader and white, forming minute patches on sterna 3 and 4 and sometimes 2; sternum 1 sometimes with two patches of broader setae medially.

*Legs:* Profemoral tooth stouter than others; metafemora thicker than those anteriorly, especially in male; metatibia in male deeply emarginate before uncus; uncus large, compressed; in female metatibia similar to meso- and protibiae, uncus usually small and acute, sometimes short and truncate, never large and compressed; femora with vestiture (usually dense apically) of oblong and elongate, brown, tan, pale tan, and white setae, many scale-like, the white and tan ones predominant; femoral bands very conspicuous when setae are white.

*Male genitalia:* (Figs. 67 and 94). Aedeagus twice as long as wide at base, and twice the length of the aedeagal struts; sides sinuate and converging apically to form a distinct, broad, rounded process, the latter usually expanded as in Fig. 67, sometimes less so; inner curvature sometimes straight medially instead of indented as shown in Fig. 67; dorsal membrane difficult to detect, especially basally, with apical border V-shaped; transfer apparatus with the median J-shaped pair of bars bordered beneath and laterally by elongate bars, the latter much longer than J-shaped ones; elongate bars and a single median bar slightly protruding into prephallotremic area, the median bar not visible in lateral view. Length .836-.988 mm., width at base .336-.411 mm., aedeagal struts .312-.399 mm.

*Neotype locality:* Topeka, Kansas. Say's type locality: "United States."

*Neotype:* Male, coll. Popenoe (WPH).

*Neallotype:* Female, Oakwood, Illinois, June 14, 1931, Frison (ISNHS).

*Neoparatypes:* CANADA: Toronto, Ontario, R. J. Crew, ♀, (USNM); Prince Edward Co., Ont., September 15, 1918, J. F. Brimley, ♂, (USNM); DISTRICT OF COLUMBIA: 1 ♂, 3 ♀ (USNM), ♂, ♀, (HFS); FLORIDA: LaBelle, July 16, 1939, Oman, ♂, (USNM); GEORGIA: Fort Valley, June 21, on peach, E. R. Selkregg, Quaintance No. 19661, ♂, (USNM); Barnesville, June 30, 1910, on peach, Quaintance 5709, ♀, (USNM); ILLINOIS: Centerville, Sangamon River, August 16, 1914, ♂, (ISNHS); Carbondale, June 10, 1904, jarred from apple, Ac. No. 34745, Taylor, ♀, (ISNHS); Northern Illinois, June 2, Peabody Coll., 2 ♀, (ISNHS); E. St. Louis, Rose Lake, July 19, 1906, ♀, (HFS); Willow Springs, June 14, 1912, ♀, ♂, (HFS); IOWA: Henry Co., May 21, 1936, Knutson, ♂, (IISC); Lake Okoboji, June 24, 1916, L. L. Buchanan, ♂, (USNM); Iowa City, Wickham, ♂, (USNM); KANSAS: Topeka, Popenoe, ♀, ♂, (USNM), ♀, (HFS); Riley Co., Popenoe, ♀, (USNM), ♀, (WPH); Onaga, Wickham, ♂, (HFS); LOUISIANA: New Orleans, August 2, 1904, U. S. D. A. 8583, Graybill, ♂, (USNM), ♂, (HFS); MARYLAND: College Park, July 20, 1921, bred from *Aquilegia*, H. S. McConnell, ♂, (USNM), ♂, (HFS); Beltsville, July 10, 1919, L. L. Buchanan, ♀, (WPH); MASSACHUSETTS: Melrose High, May 30, 1908, D. H. Clemons, ♀, (USNM); MISSISSIPPI: Natchez, June 3 and 7, 1909, at light, E. S. Tucker, ♂, ♀, (USNM); Meridian, H. Soltau, ♀, (USNM); MISSOURI: St. Louis, June 24, 1938, U. S. D. A. Traps, ♂, (HFS); Kansas City, 25.5, H. Soltau, ♀, (USNM); Missouri, C. V. Riley, ♀, (HFS); Caleb, May 24, 1885, J. S. Barlow, ♀, ♂, (USNM); MONTANA: 2 ♀, (HFS); NEW JERSEY: Coll. F. H. Chittenden, ♂, (USNM); NEW YORK: New York City and vicinity, ♂, (USNM); OHIO: Chagrin Falls, May 20, 1935, Host, Columbine, larvae in stems, C. R. Neiswander, ♀, (USNM); OKLAHOMA: Vinita, Indian Territory, June 7 and 8, 1899, Wickham, ♂, (USNM); TEXAS: Columbus, Hubbard and Schwarz, ♂, (USNM); Texas, ♀, (USNM), ♀, (HFS); Victoria, October, 1913, found in cotton squares sent from Tallulah, La., B. R. Coad, ♂, (USNM); VIRGINIA: Black Pond, June 28, 1935, Wash., D. C., H. S. Barber, ♀, (USNM); Fredricksburg, May 2, 1900, W. D. Richardson, ♂, ♀, (USNM); Great Falls, August 24, 1919, L. L. Buchanan, ♂, (USNM); Nelson County, June 26, 1914, W. Robinson, ♀, (USNM); WEST VIRGINIA: West Sulphur, July 18, 1914, W. Robinson, ♀, (USNM); Kanawha Sta. July 6, 1905, Hopkins 6036b, Mulberry, ♀, (HFS).

*Distribution:* "Ranges from New England to Michigan and Iowa, south to Florida and Texas," Blatchley and Leng (1916). Range extended west to Montana. Records from states other than those previously listed: Kentucky, Maine, Michigan, North Carolina, and Wisconsin.

**Biology:** *C. anaglypticus* (Say) has recently been considered as an economic pest of peach in the south (Peairs, 1941, and Snapp, 1930). The curculio, however, has a wide range of hosts of which peach is by no means the most preferred.

Brooks (1924) states that the larva of this species attacks peaches, cotton bolls, and the cambium and inner bark of various fruit and shade trees. The latter method of attack has given the insect the name "cambium curculio." Trees become infested at breaks or wounds in the bark, 20 to 38 larvae sometimes feeding at the edge of a single wound. Infested wounds are enlarged, and their healing is retarded or prevented by the feeding of the larvae. Brooks found larvae feeding at bark wounds on apple, pear, pignut (*H. glabra*), American hornbeam, sweet birch, American beech, American chestnut, white oak, chestnut oak, red oak, tulip tree, service berry, red maple, tupelo, flowering dogwood, and sourwood. Very little host preference was shown by the curculio although apple and pear were especially attractive.

Snapp (1930) reports jarring *anaglypticus* (Say) and *nenuphar* (Hbst.) from peach trees, the latter being greatly predominant. This worker definitely proved that the cambium curculio injures sound peaches, the previous conclusion having been that peaches, to be infested, must be bruised or wounded. In Georgia there are two generations per year of *anaglypticus* (Say); its life-history is closely similar to that of *nenuphar* (Hbst.). Brooks (1924) records one generation per year in West Virginia.

Specimen as well as literature records show that this species also breeds in cotton bolls in Louisiana. According to T. H. Jones (Brooks, 1924), the larvae feeding in the bolls seem to prefer to work around the stem ends. Jones found the larvae fairly common in bolls, but was unable to decide whether they caused the primary injury or follow other injury. Folsom (1936a) reports that at Tallulah the adults feed on the squares in July and August, making them turn yellow and fall.

A new host plant for *anaglypticus* (Say) is columbine (*Aquilegia*). Both H. S. McConnell, College Park, Maryland, and C. R. Neiswander, Chagrin Falls, Ohio, have bred specimens from this plant. The larvae of the Ohio specimens were in the stems of the plant.

Other specimen records reveal possible additional hosts: "feeding on cowpea" (Baton Rouge, La., C. E. Smith); "on *Crataegus* and plum" (Opelousas, La., R. A. Cushman); "on Japanese plum, flower buds" (Belle Chasse, La.); "on diseased elm" (Morristown, N. J., H. Hoffman); and "mulberry" (Kanawha Sta., W. Va., A. D. Hopkins).

Records from Indiana, Maryland, North Carolina, District of Columbia, Texas, and Delaware reveal that *anaglypticus* (Say) is attracted to light.

Brooks (1924) indicated that two parasites, *Thersilochus conotracheli* Riley (Hymenoptera) and *Myiophasia globosa* Townsend (Diptera), probably attack the larvae of the cambium curculio.

*Remarks:* *C. anaglypticus* (Say) is common in the midwestern area, being present in all the collections studied. The two yellowish oblique bars on the elytra make this species one of the easiest to recognize of all species of *Conotrachelus*. It is most closely related to *leucophaeatus* Fahr.

### *Conotrachelus leucophaeatus* Fahreus

*Conotrachelus leucophaeatus* Fahreus, 1837, Schönh. Gen. Spec. Curc., IV, pt. 1, p. 417; Leconte and Horn, 1876, Rhynchophora N. A., Proc. Amer. Philos. Soc., XV, No. 96, p. 234; Champion, 1904, Biol. Cent. Amer., IV, pt. 4, p. 394; Blatchley and Leng, 1916, Rhynchophora N. E. Amer., p. 481; Mutchler and Weiss, 1925, Conotr. N. J., Circ. 87, Bur. Stat. and Insp., Dept. Agr., N. J., p. 19.

*Conotrachelus demens* Boheman, 1837, Schönh. Gen. Spec. Curc., VIII, pt. 2, p. 31.

*Length:* 3.8-5.4 mm.

*Special characters:* Eyes contiguous beneath or nearly so; interocular distance not greater than twice the diameter of a facet; prothoracic furrow broad, bordered on each side by a distinct ridge; disc with a longitudinal, median carina, deeply and roughly punctate; white elytral band bordered basally and apically by brownish areas.

*Color:* Elytra reddish-brown mixed with black; apical declivity light reddish-brown; prothorax dark reddish to piceous.

*Head:* Punctures dense, coarser apically; rugulose; practically bare; groove above eye sometimes densely set with tannish setae; a few broader white setae usually present at middle; beak feebly curved; curvature abrupt near antennal insertion; subequal in length to prothorax and in both sexes; trisulcate laterally between base and antennal insertion; sulci in male usually distinct; in female the upper and median sulci frequently feeble or evanescent; sulci punctate; dorsal surface in male with an acute carina from base to distad of middle; carina either present or absent in female; dorsal tip distad of antennal insertion with elongate punctures, dense and coarse or sparse and fine; surface densely rugulose, especially evident when sulci are obscure; sulci sparsely set with chiefly pale tan or brown setae; several broader, more evident, reddish-yellow or white setae in the lower sulcus basally and at the dorsal point of junction of beak and eye; antennae inserted one-fourth to one-third before apex.

*Prothorax:* Slightly wider than long; sides subparallel to near apex, then constricted; ridges bordering median furrow sometimes tuberculate at their posterior points; densely punctate with large, deep pits; the prominent median longitudinal carina extending from before base anteri-

only into furrow, ending subapically, usually stoutest basally, tending to be finer and evanescent apically, either straight or tortuous; densely rugulose; sparsely clothed with reddish-yellow, tan, brown, and white recumbent to suberect setae varying in length, sometimes recurved; the shorter white (sometimes mixed with tannish) setae on each side forming a sinuate line from basal angle diagonally to postocular lobe; white setae also forming a variable prominent pattern above this line; usually two branches of this pattern unite with diagonal line, one apically, the other at basal angle so that an irregular triangle is formed; usually one basal and two apical branches complete this pattern; the longer reddish-yellow and pale white setae sparsely but usually conspicuously interspersed in pattern.

*Elytra*: Nearly three-fourths as wide at the base as long; sides subparallel for more than half, then gradually converging to apex; sometimes convergence abrupt; basal border feebly emarginate before the humeri; the latter not prominent, rounded; interval 3 moderately costate, with costa most evident posteriorly, sometimes interrupted anteriorly or both anteriorly and posteriorly; elevations feeble; interval 5 with a feeble to moderate costa, interrupted subbasally; intervals 7 and 9 feebly costate; serial punctures coarse; moderately dense to dense vestiture, chiefly of recumbent white and pale white setae which cover elytra in a broad band from behind humeri to apical declivity; setae densest in an oblique stripe through subbasal interruption of costa of interval 5; setae usually less dense elsewhere, particularly in discal area between third intervals; elytral area anterior to white band with sparse covering of mainly reddish-yellow and reddish-brown setae which are condensed on humeri and on intervals 3 and 5, especially 3; brownish setae usually forming a dark spot on interval 3 behind the middle and frequently on interval 2; apical declivity sparsely covered with mostly reddish-yellow and reddish-brown setae; intervals frequently set with tan and white subrecumbent setae, usually more evident on alternate intervals; vestiture frequently obscuring serial punctures and costae.

*Ventral surface*: Anterior border of mesosternum triangulate or straight, varying in prominence; metasternum with a ridge from meso- to metacoxa. Abdominal sterna 1, 2, and 5 densely and coarsely punctate; sterna 3 and 4 with punctures sparser and usually larger than those of sterna 1, 2, and 5; coarseness of punctures varying in different specimens; sternum 5 without tubercles or depressions; abdominal surface densely rugulose; each puncture with a fine amber or brownish seta; lateral setae on sterna 2, 3, and 4 broader and white, tan, or reddish-yellow, forming conspicuous patches; also a patch of broader setae on apical border of sternum 1 on each side of middle.

**Legs:** Femora with a tooth and denticle; metaunci in both sexes nondentate; apical half of femora with moderately dense to dense vestiture of white, yellow, and brown setae; metafemora more conspicuously banded than others, color usually white.

**Male genitalia:** (Figs. 68 and 95). Aedeagus elongate, approximately three times as long as wide at base, and approximately three times the length of the aedeagal struts; sides bisinuate and abruptly curving at apex to form an elongate process; outer curvature sometimes less abrupt and apical process wider than in Fig. 68; dorsal membrane elongate, with apical border V-shaped; transfer apparatus distinctly projecting into prephallotremic area; laterally both dorsal and ventral curvatures depressed medially. Length 1.125-1.312 mm., width at base .351-.375 mm., aedeagal struts .312-.375 mm.

**Type locality:** Mexico.

**Type:** Fahreus Collection, Stockholm Museum, Stockholm, Sweden.

**Distribution:** Ranges from Wisconsin and Indiana to Colorado, south to Alabama, Texas, Arizona, and Mexico. Mutchler and Weiss (1925) mention two records from New Jersey, and Brimley (1938) one from North Carolina. The specimen upon which the Brimley's record was based has on examination proven to be *obesulus* Hust., and the New Jersey records are questionable in view of the species' rather limited southern and western distribution. Records from Arizona, Colorado, Kansas, Oklahoma, Texas, and Wisconsin.

**Biology:** Specimen labels show that *leucophaeatus* Fahr. has been taken frequently on *Euphorbia marginata* in Texas and Kansas. Pierce (1907a) reports that it breeds in the stems of this weed, the larvae being present throughout the summer. Blatchley and Leng (1916), in quoting Pierce, erroneously give the species as *E. corollata*.

A second definite host is *Argemone*, prickly poppy, specimens of *leucophaeatus* Fahr. having been bred from this plant by S. G. Kelly at Manhattan, Kansas. It has also been collected on *Argemone mexicana* by R. A. Cushman at Hallettsville, Texas.

Other specimen records reveal that *leucophaeatus* Fahr. frequents cotton and milkweed: "*Asclepias* sp." (Childress, Texas, J. D. Mitchell); "on milkweed" (Victoria, Texas, B. R. Coad); "collected on cotton" (Chillicothe, Texas, E. S. Tucker); "on cotton, apparently feeding on cotton squares" (Victoria, Texas, W. D. Hunter); and "on cotton squares" (10 mi. N. E. Uvalde, Texas, O. C. Parman). Pierce (1907a) reports it being taken on cotton at Victoria, Denton, Runge, and San Antonio, Texas, on corn at Dallas, and on *Quercus* at Gurley. Sanderson (1904) states that *leucophaeatus* Fahr. breeds in stems of *Amaranthus*, but this record has not since been substantiated.

This species has also been collected "at lights" in Kerrville, Texas, and Durant, Oklahoma.

*Remarks:* *C. leucophaeatus* Fahr. is typically a southwestern species, rarely being found in the eastern half of the United States. Champion (1904) states that it is quite common in Mexico, and Blatchley and Leng (1916) report it abundant in Texas.

This species is closely allied to *obesulus* Hust., of which only a few specimens have been collected. *C. obesulus* Hust. was originally described by Fall as *obesus* in 1917, but Hustache in 1936 pointed out its preoccupation by *obesus* Pascoe 1881 and erected the new name. Fall, in his original description, stated that *obesulus* Hust. and *anaglypticus* (Say) have a close affinity, and that the two are differentiated mostly by *anaglypticus* (Say) having its costae non-interrupted in comparison to *obesulus* Hust. which has the costae of intervals 3 and 5 interrupted anteriorly. The costa of interval 5 in *anaglypticus* (Say), however, is always distinctly interrupted anteriorly; so whether Fall really had *anaglypticus* (Say) in mind when he wrote this statement is somewhat questionable. The type of *obesulus* Hust., seen in Fall's Collection at the Museum of Comparative Zoology, resembles *leucophaeatus* Fahr. very much except that it is extremely broad and robust in comparison to that species. Unfortunately, most of its vestiture is rubbed off so that it looks unnaturally bare. A male specimen of *obesulus* Hust. from Southern Pines, North Carolina, has the aedeagus with the lateral plates gradually converging apically to form the apical process in contrast to the abrupt convergence in *leucophaeatus* Fahr. (Fig. 68). The prothoracic ridges in this specimen are less evident than those in *leucophaeatus* Fahr., and the eyes are less contiguous. With only one specimen of *obesulus* Hust. at hand, however, the writer hesitates to enumerate differences between the two species. More specimens of *obesulus* Hust. are necessary for examination before definite characters for the differentiation of the two species can be set up. For the present the more robust form and less contiguous eyes of *obesulus* Hust., plus the previously mentioned aedeagal difference, will serve for the separation of the two species.

#### GROUP IV

This group includes Divisions III and IV of Leconte and Horn (1876) and Groups V and VI of Blatchley and Leng (1916). It comprises those species of *Conotrachelus* which have the tarsal claws approximate and deeply cleft. In the North Central States two species of Group IV are present, *erinaccus* Lec. and *fissunguis* Lec. The previously quoted writers, however, put each of these species in a different group, although both are closely linked by their tarsal affinities. The principal differ-

ence stated by Blatchley and Leng between the two species, and thus between the two groups, is that Group V has a prostrate fine pubescence mixed with short bristles, whereas Group VI has the pubescence mixed with fine, stout bristles.\* Other subordinate differences listed are: Group V has the beak as long as the head and thorax, carinate and coarsely striate on the basal two-thirds; antennae inserted one-fifth from its tip; elytra with rows of very short bristles; and tarsal claws cleft at the tip. Group VI has the beak rather slender, longer than the head and thorax, feebly striate, finely and sparsely punctate; elytra with long, stout, erect bristles; and tarsal claws deeply cleft. Of these contrasting characters, the differences in the type of bristles and the length of the beak appear to be the most reliable ones. The other characteristics are either equally applicable to both groups, or as in the case of the difference in the punctuation of the beak, not of group significance. Just what is meant by Blatchley and Leng's statement that the tarsal claws in *fissunguis* Lec. are cleft at the tip is not clear, since the claws of both species are equally cleft.

The question then arises whether the two characters mentioned, the "bristles" and the beak, are of group significance. In the writer's opinion they are not. The beak varies greatly in relative length, as in Group I where in the female of *affinis* Boh. it attains the abdomen, in *nenuphar* (Hbst.) and *albicinctus* Lec. it barely reaches the mesosternum, and in *seniculus* Lec. and *nivosus* Lec. it is subequal to the prothorax in length. "Bristles" likewise vary within the other groups, as in Group II where *cribricollis* (Say) has stout, erect "bristles" similar to those of *erinaceus* Lec. while *geminatus* Lec. has much finer and shorter ones. Consequently, it would appear that if the above differences are used in one place to set up groups, such differences should not be ignored in other places. Because of these facts, Groups V and VI of Blatchley and Leng have, therefore, been consolidated into one. It may be pointed out that since these groups were originally erected for convenience of treatment, it might be well to retain the division. This does not apply since the treatment of the two species in question is just as convenient when included under one group as when under two. In addition, a one-group classification shows that there is a closer relationship between these two species than there is between either of these species and any species of the other groups.

Group IV is characterized chiefly by its approximate, cleft tarsal claws. Other characteristics are: beak feebly curved; first two funicular segments of antennae subequal in length and longer than any of the others; prothorax wider than long, coarsely and densely punctate, punc-

\*The term, "bristles," is synonymous with the term suberect or erect setae used in the descriptions of the species in question. It is used above, however, to facilitate discussion. The setae, in the writer's opinion, are too broad to be called "bristles."

tures with suberect to erect setae; elytral intervals not costate and with suberect setae; mesoscutellum from lateral aspect abruptly declivent basally; metasternum not grooved from meso- to metacoxa in either sex; femora with a single tooth; aedeagus elongate, depressed apically, with a dorsal membrane and an apical process; transfer apparatus with two or more pairs of sclerotized bars.

## KEY TO SPECIES OF GROUP IV

1. Elytra with suberect setae of intervals only slightly longer than recumbent setae; prothorax bare except for short suberect setae arising singly from punctures; aedeagus as in Fig. 65.....*fissunguis* Lec., p. 131
- 1- Elytra with suberect setae of intervals from two to three times as long as recumbent setae or scales; prothorax with numerous scattered scale-like setae or scales in addition to the long suberect setae arising from the punctures; aedeagus as in Fig. 64.....*erinaceus* Lec., p. 134

*Conotrachelus fissunguis* Leconte

*Conotrachelus fissunguis* Leconte, 1876, Rhynchophora N. A., Proc. Amer. Philos. Soc., XV, No. 96, p. 234; Blatchley and Leng, 1916, Rhynchophora N. E. Amer., p. 481; Mutchler and Weiss, 1925, Conotr. N. J., Circ. 87, Bur. Stat. and Insp., Dept. Agr., N. J., p. 19.

*Length:* 4.2-5.4 mm.

*Special characters:* Elytra with a median, discal, subglabrous, blackish area; profemur with a distinct anterior bulge opposite femoral tooth; similar bulge absent on meso- and metafemora; abdominal sterna 3 and 4 with punctures dense and present over the entire area.

*Color:* Elytra reddish-brown with areas of black at middle on disc and along sides, and on anterior face of humeri; prothorax piceous, darker than elytra.

*Head:* Densely punctate; punctures with tan and pale setae, sometimes scarcely visible unless highly magnified; beak stout, feebly curved; curvature more abrupt near antennal insertion; beak as long as prothorax, subequal in length in both sexes, trisulcate laterally between base and antennal insertion; lower and median sulci distinct, the upper one feeble and obscure, sometimes replaced by dense punctures; dorsal surface occasionally feebly carinate proximad of antennal insertion; tip distad of antennal insertion with dense elongate punctures, frequently coalescing and forming small sulci; sparse pale tan setae in lateral sulci; antennae inserted approximately one-fourth from apex.

*Prothorax:* Sides feebly rounded from base to apex or subparallel with a feeble subapical constriction; disc densely and coarsely punctate; punctures deep, frequently confluent and forming longitudinal ridges, the most prominent and constant of which is a median one; this ridge some-

times absent, its length variable; virtually bare except for short, inconspicuous, suberect or erect, pale tan or brown setae in punctures, one to each puncture.

*Elytra*: More than three-fourths as wide as long; sides subparallel for more than half, then gradually converging to apex; sometimes entire outline rounded from base to apex, the curvature feeble basally; basal border emarginate before humeri, the latter not prominent and rounded; intervals flat; sometimes intervals 3, 5, 7, and 9 very feebly convex; serial punctures coarse; with a moderate to dense covering of pale tan, or white and tan, recumbent setae except in blackish areas; setae in these areas sparse, the areas bare in appearance, specimens usually rubbed and frequently with elytra subglabrous in numerous areas; setae darker subapically; intervals each set with a row of white and tan, short, suberect setae, more evident posteriorly, frequently difficult to see.

*Ventral surface*: Mesosternum feebly angulate anteriorly. Abdominal sterna with dense coarse punctures, small considering size of species; sternum 1 occasionally less densely punctate than others; sternum 5 without tubercles and usually without depressions (one specimen with a median transverse depression); punctures usually with short, fine, obscure, amber setae, occasionally replaced by broader, white, or tan, easily observed setae, the latter when present usually on sterna 1 and 2 and along sides of 3 and 4.

*Legs*: Femoral tooth usually feeble; metaunci not dentate in either sex; female usually but not always with a tooth on outer apical edge of metatibia opposite the uncus; legs sparsely covered with tan and reddish-yellow setae, densest apically on femora.

*Male genitalia*: (Figs. 65 and 92). Aedeagus twice as long as wide at base, and three times as long as aedeagal struts; sides feebly sinuate and gradually converging at apical third to form a process; inner curvature evanescent basally, varying in distinctness in individual specimens; dorsal membrane narrowed to near base, then expanded; apical border V-shaped; transfer apparatus with a pair of sinuate bars bordering a median pair of feebly curved ones, the latter approaching apically to form a broad V; laterally, ventral curvature sometimes not as abrupt as in Fig. 92. Length 1.14-1.18 mm., width at base .461-.500 mm., aedeagal struts .351-.375 mm.

*Type locality*: Southern States (Louisiana, according to Leconte, 1876).

*Lectotype*, hereby designated: Museum of Comparative Zoology Type No. 5220-2, J. L. Leconte Collection (MCZ).

*Lectoparatypes*: ~~Museum of~~ Museum of Comparative Zoology Type No. 5220-3, Southern States; J. L. Leconte Collection (MCZ). Museum of Com-

parative Zoology Type No. 5220-1, no locality, but probably same as above since species was described from three Louisiana specimens; J. L. Leconte Collection (MCZ).

*Distribution:* "Ranges from New Jersey and District of Columbia to Louisiana," Blatchley and Leng (1916). Range extended west to Missouri, Illinois, and Texas. Records from: District of Columbia, Illinois, Louisiana, Maryland, Missouri, New Jersey, Pennsylvania, Texas and Virginia.

*Biology:* Pierce (1907a) and Blatchley and Leng (1916) record *fissunguis* Lec. as breeding in the swamp rose mallow, *Hibiscus moscheutos* L. Weiss and Dickerson (1919) from studies on the biology of this species on *H. moscheutos* report that the curculio's attacks appear to be confined to the seed capsules of *Hibiscus*. Since then this species has become known as the hibiscus seed capsule curculio.

In New Jersey, according to Weiss and Dickerson (1919), the curculio passes the winter in the adult stage, appearing the following year in July. These adults feed at the base of the flower petals, the females beginning oviposition as soon as the seed capsules are formed. The eggs are deposited in the seed capsules, being inserted through irregular circular punctures in the wall. Some capsules are punctured as many as eighteen times, others only two or three times. The newly hatched larva bores into the developing seed and feeds upon it until only the outer shell remains. When too large to enter the seeds, the larva consumes them from the outside. On attaining full growth, the larva leaves the capsule by cutting a circular hole through the wall or by merely crawling out if the capsule has split open. After dropping to the ground, it burrows one-half to one inch below the surface of the soil for pupation. From laboratory data, Weiss and Dickerson (1919) found that the larvae entered the soil on August 27, pupated on September 2, and transformed to the adult stage on September 18. For several days the adults remained in the soil, issuing on and after September 22. These adults then went into hibernation until the following summer. Weiss and Dickerson (1919) found infested seed capsules only on plants bordering a marsh. This was explained on the basis that marsh ground itself, being almost constantly wet, would hinder successful pupation.

Specimen records reveal that other species of mallow are also attacked: "bred from *H. lasiocarpus*" (Baton Rouge, La., T. H. Jones); "in seed of *H. militaris*" (District of Columbia; and "bred *H. militaris* pod" (Mitchener, La.). In Louisiana, specimens were bred as early as July 30, and this suggests that the life history in the southern states may be slightly different from that in New Jersey.

L. Haseman also found this species on wild cotton at Malden, Mis-

souri. It has been collected "at lights" at Wharton, Texas, and Washington, D. C.

*Remarks:* *C. fissunguis* Lec. is fairly common in Illinois.

*Conotrachelus erinaceus* Leconte

*Conotrachelus erinaceus* Leconte, 1876, Rhynchophora N. A., Proc. Amer. Philos. Soc., XV, No. 96, p. 235; Blatchley and Leng, 1916, Rhynchophora N. E. Amer., p. 482.

*Length:* 2.85-3.35 mm.

*Special characters:* Apical half of head densely covered with scales or scale-like setae; elytral vestiture dense, composed chiefly of recumbent scales; abdominal sterna 3 and 4 each with a row of coarse, closely set punctures.

*Color:* Elytra reddish-brown, with several splotches of black; prothorax dark reddish-brown to piceous.

*Head:* Densely punctate and thickly covered with reddish-yellow, tan, and white scale-like setae or scales on the apical half; basal half with scale-like or oblong setae, much sparser than on apical half; beak feebly curved, longer than prothorax, slightly longer in female than in male, slightly stouter in male; trisulcate laterally between base and antennal insertion; upper sulcus feeble, especially in the female where it is replaced subapically by fine punctures; dorsal surface sometimes with a feeble rounded ridge, distad of antennal insertion with fine, sparse to moderately dense punctures, usually sparse in female; sulci with a few tan and white, elongate setae; setae more scale-like and denser dorsally between the eyes; antennae inserted one-third to one-fourth from apex, in male nearer one-fourth.

*Prothorax:* Sides subparallel or feebly rounded, constricted subapically; disc with large, deep, and dense punctures, the latter sometimes confluent; non-carinate; white and tan recumbent scale-like setae or scales scattered over disc, sometimes condensed longitudinally at middle and along sides; each puncture with a suberect or erect white, tan, or dark brownish seta.

*Elytra:* Approximately one-fourth longer than wide; sides parallel for more than half, then gradually converging to apex; basal border feebly emarginate before humeri; the latter not prominent, rounded; intervals not costate, at the most feebly convex; serial punctures coarse, mainly hidden by vestiture; the latter a dense mixed covering of white and tan scale-like recumbent setae or scales, tan scales usually predominant; each interval with prominent, elongate, suberect setae ranging from white and tan to dark brown, or black; setae sometimes absent basally, especially on intervals 2, 4, and 6.

**Ventral surface:** Mesosternum triangulate anteriorly. Abdominal sterna with coarse punctures; sterna 1 and 5 moderately to densely punctate; sternum 2 usually more sparsely punctate, sometimes with a smooth transverse median area; sterna 3 and 4 with a transverse row of closely-set punctures; sternum 5 without tubercles or depressions; each puncture with an elongate, recumbent to suberect, tan or white seta; lateral, recumbent, white setae on sterna 3 and 4 forming small patches.

**Legs:** Femora with a small tooth; metaunci dentate in male only; metatibiae in both sexes with a denticle on outer margin of apex, opposite the uncus; legs with a sparse covering of white and tan, recumbent and suberect setae, some scale-like, others elongate; vestiture denser on apical half or third of femora.

**Male genitalia:** (Figs. 64 and 91). Aedeagus two and one-half to three times as long as wide at base, and approximately five times the length of the aedeagal struts; sides sinuate; abruptly curved one-third before apex to form an elongate process; dorsal membrane narrowed basally; membrane variable in its basal extension; apical border broadly V-shaped; transfer apparatus consisting of three pairs of bars; the basal and most evident pair with apical tips approaching medially to form a broad U. Length .851 mm., width at base .274-.298 mm., aedeagal struts .149-.161 mm.

**Type locality:** "Southern States."

**Lectotype**, hereby designated: Museum of Comparative Zoology Type No. 5219-2, J. L. Leconte Collection (MCZ).

**Lectoparatypes:** Museum of Comparative Zoology Type No. 5219-3, Texas, J. L. Leconte Collection (MCZ); Museum of Comparative Zoology Type No. 5219-1, no locality, J. L. Leconte Collection (MCZ).

**Distribution:** "Ranges from Ohio and Northern Indiana to District of Columbia, Florida and Texas," Blatchley and Leng (1916). Extension of range north to New York, and west to Missouri and Kansas. This species is recorded by Blatchley and Leng (1916) as frequent in southern Indiana but scarce in the northern area of that state. From this literature record and specimen records, it appears that *erinaceus* Lec. cannot survive in large numbers in the more northern sections of the United States. Only one record (Turin, N. Y.) shows this species occurring farther north than 42.5° latitude. Records from: Alabama, Arkansas, District of Columbia, Florida, Georgia, Illinois, Kansas, Kentucky, Louisiana, Missouri, New York, Ohio, Oklahoma, Tennessee, Texas, Virginia.

**Biology:** Literature and specimen data reveal this species as a pest of cotton. Folsom (1936a and b) reports this curculio common in cotton

fields at Tallulah, Louisiana, from late May to September. He states that the curculios usually occur in the bud clusters of the cotton plant, where they eat into the buds and kill them. Many young squares are blasted while the older squares are caused to flare, turn yellow, and drop. The curculio also feeds on the stems and leaves, killing the latter by cutting into the petioles. In some instances small plants are also killed.

Folsom's data on *erinaceus* Lec. are substantiated by the available specimen records. The species has been recorded "on cotton" or "in cotton fields" at Dancy, Agricultural College, Kosciusko, Thornton, Clarksdale, Vicksburg, McCool, Port Gibson, Holly Bluff, and Natchez, Mississippi; at Blossom, Texas; at Henryette, Oklahoma; at Tallulah, Louisiana; and at Richland, Paragould, and Clarksville, Arkansas. More definite records are: "from cotton bud" (Wharton, Texas, R. L. McGarr); "injuring cotton buds" (Knoxville, Tenn., S. Marcovitch); and "kills tops of seedling cotton plants by punctures below cotyledon" (Knoxville, Tenn., D. M. Simpson). The last two records and the work reported by Folsom show definitely that cotton serves as a food source for *erinaceus* Lec. Whether the curculio actually breeds in the cotton, however, has not been revealed by these data.

Other miscellaneous specimen records are: "on Aster sp." (Wolfe City, Texas, F. C. Bishopp); "on Rubus" (Lafayette, La., R. A. Cushman); "Timothy seed" (Charleston, Mo., Satterthwaite); and "at light" (Tallulah, La., and District of Columbia). Pierce (1907a) reports taking *erinaceus* Lec. on *Baptisia* at Greenville, Texas.

*Remarks:* *C. erinaceus* Lec. is common in Illinois. It is easily recognized by its approximate cleft tarsal claws, and its prominent subrect elytral setae.

## VII. ADDENDUM

*Conotrachelus carolinensis* n. sp. does not occur in the area studied and therefore is included as an addendum. This species belongs to Group III by virtue of its dorsal prothoracic furrow. It can be readily separated from *tuberosus* Lec. by the costal character of couplet 1 in the key (p. 119). For further separation in Group III the key must be modified as follows:

2. Elytral vestiture usually not conspicuously white; if so, transverse whitish band is behind subbasal interruption of costa of interval 5, and each elytron has an oblique bar of yellowish vestiture behind humerus; male metatibia with apical emargination (Fig. 32a and b)..... 3
- 2- Elytral vestiture conspicuously white, a broad transverse white band extending from apical declivity to humerus; elytron never with an oblique yellow bar posterior to humerus; male metatibia not emarginate apically; aedeagus as shown in Figs. 68 and 95.... *leucophaeatus* Fahreus, p. 126

3. Each elytron with an oblique bar of yellowish vestiture extending postero-medially through subbasal interruption of costa of interval 5; bar usually distinct, sometimes faint, but always evident; prothoracic furrow usually feeble, rarely bordered by distinct carinae; apical emargination of male metatibia deep as shown in Fig. 32a; aedeagus as shown in Figs. 67 and 94; the J-shaped and elongate bars of transfer apparatus as shown in Fig. 107.....*anaglypticus* (Say), p. 121
- 3- Elytron never with an oblique bar of yellowish vestiture; oblique area across subbasal interruption of costa of interval 5 with short white recumbent setae, usually sparse; prothoracic furrow bordered on each side by distinct carinae; apical emargination of male metatibia shallower as shown in Fig. 32b; aedeagus as shown in Figs. 100 and 106; the J-shaped and elongate bars of transfer apparatus as shown in Fig. 104 .....*carolinensis* n. sp., p. 137

*Conotrachelus carolinensis* n. sp.

*Length:* 2.55-3.80 mm.

*Special characters:* Eyes contiguous beneath or nearly so; interocular distance at the most 2-3 times the diameter of a facet; median furrow of prothorax distinct; lines of yellowish vestiture at base of elytral interval 3 conspicuous; the J-shaped and elongate bars of transfer apparatus as shown in Fig. 104.

*Color:* Elytra chiefly reddish-brown with splotches of black, prothorax reddish to black.

*Head:* Coarsely, densely, and roughly punctate; punctures larger apically; densely rugulose; setae in punctures usually inconspicuous except along midline and above eyes; beak stout, curved; curvature usually more abrupt just above the antennal insertion; beak shorter than or subequal to prothorax; trisulcate laterally between base and antennal insertion; upper and median sulci occasionally evanescent basally; sulci sometimes less distinct in female; dorsal surface acutely carinate from base to distad of middle; carina occasionally rounded in female; tip distad of carina in male with dense elongate punctures, in female punctures usually finer and sparse; sulci sparsely set with reddish-yellow, tan, and white setae, sometimes scale-like setae also present; antennae inserted approximately one-third before apex; first and second funicular segments subequal in length, first stouter than second, each longer than any of remaining segments.

*Prothorax:* Usually wider than long (one specimen with length equal to width); sides subparallel or gradually widening to before apex, then constricted; densely, coarsely, and roughly punctate; carinae bordering median furrow frequently tortuose, sometimes interrupted by punctures; posterior end of carinae sometimes tuberculate; disc sometimes with a median longitudinal carina; densely rugulose; a sparse vestiture

of reddish-yellow, pale brown, tan, pale white, and white, recumbent to suberect, elongate setae; the shorter white setae forming on each side a diagonal line from basal angle to postocular lobe; above this line white setae forming an irregular pattern, usually consisting of five short lines all converging laterally at approximately the middle; this arrangement frequently obscure in dirty rubbed specimens, otherwise conspicuous; the majority of the remaining setae arising singly from punctures.

*Mesoscutellum:* From lateral aspect abruptly declivent basally.

*Elytra:* Three-fourths to four-fifths as wide as long; sides subparallel for more than half, then gradually converging to apex; basal border feebly emarginate mesad of humerus; the latter rounded, feebly prominent; intervals 3, 5, 7, and 9 moderately to acutely costate; costa of interval 3 usually complete, sometimes feebly interrupted anteriorly or posteriorly or both; if twice interrupted, the elevations formed are feeble; costa of interval 5 interrupted once anteriorly; costae of intervals 7 and 9 complete, that of 7 sometimes evanescent near the humerus, that of 9 frequently less acute than costae of intervals 3, 5, and 7; serial punctures coarse, closely set; sparse vestiture of brown, tan, yellow, and white, short to elongate, recumbent setae; the white setae sometimes predominant; setae condensed basally in lines on intervals 3 and 5 and sometimes 4; base of each line composed of white setae succeeded posteriorly by reddish-yellow, yellow, or tan setae, a similar patch of vestiture across base of humerus; setae also denser at the beginning of the apical declivity; oblique area through subbasal interruption of costa of interval 5 usually very sparsely covered with short white setae; alternate intervals set, usually conspicuously, with brown, reddish-yellow, tan, and white, subrecumbent to suberect setae; those of interval 1 directed posteriorly; those of costate intervals directed toward costal crest; apical declivity usually with few setae, bare in appearance.

*Ventral surface:* Mesosternum triangulate anteriorly; metasternum not grooved but with a ridge from meso- to metacoxa. Abdominal sterna with coarse, deep punctures; those of 1 and 5 dense; those of 2, 3, and 4 varying from sparse to dense; punctation of 3 and 4 usually less dense than that of 2; the latter usually with finer punctures basally, a row of larger ones apically; punctures of sterna 3 and 4 usually large and frequently arranged in a transverse row; sterna densely rugulose; each puncture with a fine, pale brown or amber, elongate seta; lateral setae of sterna 3 and 4 broader, white or tan, forming patches; broader setae also on apical portion of sternum 1 each side of middle.

*Legs:* Femora with a tooth and a denticle; tooth usually prominent, sometimes feeble, especially on mesofemora; metafemora usually stouter than meso- and profemora; apical emargination of male metatibia fre-

quently gradual, not as abrupt as shown in Fig. 32b; metaunci in male dentate, those of female not dentate; metafemora moderately to densely clothed apically with whitish, sometimes tannish, elongate setae; meso- and profemora less densely clothed; setae of profemora usually more uniformly distributed.

**Male genitalia:** (Figs. 100 and 106). Aedeagus more than twice as long as wide at base and two to three times the length of the aedeagal struts; sides feebly sinuate and converging apically to form a process; the latter usually with sides subparallel, sometimes expanded near the apex; inner curvature with a distinct mesad extension basad of apical edge of dorsal membrane; the latter V-shaped apically; transfer apparatus with a pair of median J-shaped bars; beneath and obliquely across the outer curvature of each J-shaped bar lies an elongate bar (Fig. 104); the latter but slightly longer than the J-shaped bar, and not protruding into prephallotremic area; a median slightly sclerotized portion of apparatus prominently projecting into prephallotremic area; projecting portion visible in lateral view (Fig. 106). Length: .750-.850 mm., width at base .325-.390 mm., aedeagal struts .250-.325 mm.

**Type locality:** Garner, North Carolina.

**Holotype:** Male, United States National Museum Type No. 55134, summer, 1940, Coll. W. A. Majure, (USNM).

**Allotype:** Female, Garner, North Carolina, December 4, 1940, hibernating beneath lespedeza, grass, and composite weeds, W. A. Majure, (HFS).

**Paratypes:** ALABAMA: Pyziton, Clay Co., H. H. Smith, ♀, (USNM); ARIZONA: Globe, Duncan Coll., ♂, (USNM); FLORIDA: Dunnellon, July 12, 1939, Oman, ♀, (USNM); St. Nicholas, ♀, (USNM); Crescent City, Coll. Hubbard and Schwarz, ♂, (HFS); GEORGIA: Myrtle, May 30, 1906, jarred from peach, Quaintance No. 2361, A. H. Rosenfeld, ♀, (USNM); MARYLAND: Chesapeake Beach, June 9, 1933, mosquito trap, F. C. Bishopp, ♀, (USNM); MASSACHUSETTS: Springfield, June 28, 1903, F. Knab, ♀, (USNM); MISSISSIPPI: Agr. College, October 22, 1894, H. E. Weed, Coll. Wickham, ♂, (USNM); Meridian, Coll. H. Soltau, ♂, (HFS); New Albany, June, 1920, on peach, Quaintance No. 20707, L. Pierce, ♂, (USNM); NEW JERSEY: Woodbine, May 11, 1925, F. M. Schott, Coll. A. Nicolay, ♂, (USNM); NEW YORK: New York City and vicinity, ♀, (USNM); NORTH CAROLINA: Aberdeen, May 25, 1927, J. A. Harris, ♀, (HFS); TEXAS: Columbus, Hubbard and Schwarz, ♀, (USNM); Austin, Coll. H. Soltau, ♀, ♂, (HFS); Beeville, June 5, 1906, in cotton fields, C. R. Jones, ♂, (USNM); Texas, ♂, (USNM), ♀, (HFS); VIRGINIA: Fort Monroe, Hubbard and Schwarz, ♀, (USNM).

*Distribution:* Ranges in coastal strip from Massachusetts south to Florida, then west to Texas; also found in Arizona. Whether the distribution of this species is actually confined to eastern and southern border states is questionable, but present available records indicate such a range.

*Biology:* This species has been beaten from peach trees in Georgia and Mississippi and collected in cotton fields in Texas. These records indicate that its hosts are possibly similar in part to those of *anaglypticus* (Say).

*Remarks:* *C. carolinensis* n. sp. and *anglypticus* (Say) are very closely related and heretofore have been considered as one species. The similarity of the male genitalia (Figs. 67 and 100) and the male metatibiae (Fig. 32a and b) reveal the extent of their affinity. The aedeagi of the two species are best differentiated by the relative lengths and position of the two sets of bars in the transfer apparatus (Figs. 104 and 107). The apical process of the aedeagus in *anaglypticus* (Say) is usually as shown in Fig. 67, but occasionally it varies toward the type exhibited by *carolinensis* n. sp. (Fig. 100), and the reverse is also true. The shape of the aedeagi of the two species is different, but this difference may not be as readily detected as that of the transfer apparatus.

In addition to the characters mentioned in the keys and diagnoses, two other relative differences are of interest. First, the length of *carolinensis* n. sp. generally averages less than that of *anaglypticus* (Say), even though overlapping occurs; and, second, the prothoracic punctation of *carolinensis* n. sp. is much coarser, frequently more like that of *leucophaeatus* Fahr. than that of *anaglypticus* (Say).

## VIII. SUMMARY

The morphological and taxonomical aspects of the genus *Conotrachelus* Dejean (Coleoptera, Curculionidae) have been studied in those species occurring in Illinois and the surrounding states of Wisconsin, Iowa, Missouri, Kentucky, and Indiana. The technique for the removal and preservation of the male genitalia is discussed in detail.

The taxonomic importance of the various morphological structures is evaluated. The uncus, mesoscutellum, and metasternal grooves are structures newly employed in the taxonomy of the genus. The characters for sex determination are given. The morphology of the male genitalia of *C. nenuphar* (Hbst.) is discussed fully and is followed by a discussion of the relative taxonomic value of the component parts of the genitalia.

Dejean (1835) is shown to be the author of the generic name, *Conotrachelus*, although in all previous works Schönherr (1837) or Latreille (1835) have been accredited with it.

Twenty-eight species occur in the area studied, five of which are new: *buchanani*, *iowensis*, *hicoriae*, *hayesi*, and *tibialis*. The species of the genus are segregated into four groups, instead of the usual six as proposed by Leconte and Horn (1876) and Blatchley and Leng (1916). The description of each species is followed, as far as possible, with a discussion of its distribution, biology, phylogeny, and nomenclature. Male genitalia, as well as the usual morphological characters, are utilized in the descriptions. Illustrations of the aedeagi and of other important taxonomic structures are included. In those cases where the types have definitely been destroyed, neotypes and neoparatypes have been erected.

The description of a new species, *carolinensis*, not found in the area studied, is presented as an addendum.

## IX. GLOSSARY

This glossary has been included so that the meaning of new or perhaps unfamiliar terms used in the section on classification can be readily obtained without recourse to the section on morphology.

**Aedeagal strut**—an elongate, ventral, basal extension of the aedeagus (Fig. 2).

**Aedeagus**—the distal, heavily sclerotized portion of the phallus (Figs. 1, 8, and 9).

**Apical process**—the apex of the aedeagus when it forms a projection (Figs. 42 and 54).

**Declivent**—modified by adverb "abruptly" and used in the description of the meso-scutellum, means that mesoscutellum is sharply cut off basally as shown in Fig. 30b or more so.

**Densely punctate**—with the punctures as shown in Fig. 33.

**Distal femoral tooth**—the tooth which is located either at the middle or on the proximal slope of the apical emargination of the femur; i.e., in Fig. 98 a distal tooth would be one located distad of the tooth (the proximal femoral tooth) shown at the proximal crest of the emargination.

**Distance (a)**—the distance between the lateral apical emargination of the beak and the anterior margin of the ball of the antennal scape (Fig. 105).

**Distance (b)**—the distance between the dorsal and ventral surfaces of the beak at the position of the antennal insertion (see Fig. 105).

**Dorsal curvature**—the upper boundary of the lateral plate when viewed from the lateral aspect (Fig. 69).

**Dorsal membrane**—the membranous, dorsal area between the two lateral plates of the aedeagus (Fig. 59).

**Dorsal plate**—the lightly sclerotized, dorsal area between the two lateral plates of the aedeagus (Fig. 1).

**Elongate**—at least two and one-half times as long as wide.

**Endophallus**—an eversible sac consisting of membranous lobes and sclerotized plates or bars which, in repose, is contained within the aedeagal cavity (Figs. 4 and 5).

**Inner curvature**—the inner boundary of the lateral plate when viewed from the dorsal aspect (Fig. 42).

**Interrupted**—with reference to the elytral costae: when the crest of the costa is definitely flattened so that an acute highlight is no longer visible.

**Lateral plate**—the heavily sclerotized plate which forms a side and part of the dorsal and ventral surfaces of the aedeagus (Figs. 1, 2, and 69).

**Moderately punctate**—with the punctures as shown in the top half of Fig. 34.

**Metasternal groove**—the groove extending from the mesocoxa to the metacoxa in the males of certain species (Fig. 19).

**Mucro** (pl. mucrones)—the spine arising from the inner apical angle of the tibia, frequently lacking in males and usually inconspicuous (Fig. 20).

**Outer curvature**—the outer border of the lateral plate when the aedeagus is viewed from the dorsal aspect (Fig. 42).

**Prephallotremic area**—the area distad of the phallotreme, thus distad of the apical border of the dorsal plate or membrane (Figs. 1, 42, and 54).

**Phallobase**—the proximal portion of the phallus, typically a sclerotized ring bearing two epimeres, usually encircling the aedeagus at its base (Fig. 1).

**Phallotreme**—the opening formed by the invagination of the endophallus beneath the apex of the dorsal plate or the dorsal membrane (Fig. 5).

**Phallus**—all of the structures of the external male genitalia including the phallobase, aedeagus, endophallus, connecting membranes, and any of the processes of these parts (Fig. 1).

**Proximal femoral tooth**—the tooth which is located at the proximal crest of the apical emargination of the femur (the tooth shown in Figs. 97 and 98).

**Spinulae**—small spines found in a row at the apical end of the tibia (Fig. 20).

**Transfer apparatus**—the sclerotized plates or bars of the endophallus (Figs. 7 and 59).

**Uncus** (pl. unci)—the spine arising from the outer apical angle of the tibia (Fig. 20).

**Ventral curvature**—the lower boundary of the lateral plate when viewed from the lateral aspect (Fig. 69).

## X. LITERATURE CITED

- AGASSIZ, L. J. R.  
1842-46. Nomenclator Zoologicus. Soloduri.
- AUSTIN, E. P.  
1880. Supplement to Crotch Check List of Coleoptera of North America, pp. 1-67.
- BARBER, H. S.  
1919. Avocado Seed Weevils. Proc. Ent. Soc. Wash., Vol. 21, No. 3, pp. 53-61.  
1923. Two New *Conotrachelus* from Tropical Fruits. Proc. Ent. Soc. Wash., Vol. 25, No. 9, pp. 182-185.
- BLATCHLEY, W. S.  
1917. New or Noteworthy Coleoptera, Florida, III. Can. Ent., Vol. 49, pp. 272-279.  
1922. Notes on the Rhynchophora of Eastern North America, with Characterizations of New Genera and Descriptions of New Species. Journ. N. Y. Ent. Soc., Vol. 30, No. 3, pp. 113-127.  
1925. Notes on the Rhynchophora of Eastern North America with Descriptions of New Species, III. Journ. N. Y. Ent. Soc., Vol. 33, pp. 87-113.
- BLATCHLEY, W. S., and LENG, C. W.  
1916. Rhynchophora or Weevils of North Eastern America. Nature Publishing Company, Indianapolis.
- BRIMLEY, C. S.  
1938. The Insects of North Carolina. N. C. Dept. Agr., Div. Ent., Raleigh.
- BRITTON, W. E., and KIRK, H. B.  
1913. The Life History and Habits of the Walnut Weevil or Curculio, *Conotrachelus juglandis* Lec. Twelfth Rept. State Ent. Conn., pp. 240-253.
- BROOKS, F. E.  
1910. Snout Beetles That Injure Nuts. Univ. W. Va. Agr. Exp. Sta. Bull. 128, pp. 145-185.  
1922. Curculios That Attack the Young Fruits and Shoots of Walnut and Hickory. U.S.D.A. Bull. 1066. 16 pp.  
1924. The Cambium Curculio, *Conotrachelus anaglypticus* Say. Journ. Agr. Res., Vol. 28, No. 4, pp. 378-386.
- BUCHANAN, L. L.  
1937. Notes on Curculionidae. Journ. Wash. Acad. Sci., Vol. 27, No. 7, pp. 312-316.
- CASEY, T. L.  
1892. Coleopterous Notices IV. Ann. N. Y. Acad. Sci., Vol. VI, pp. 359-712.  
1910. On Some New Species of Balanini, Tychiini, and Related Tribes. Can. Ent., Vol. 42, No. 4, pp. 114-144.
- CHAMPION, G. C.  
1904. Biologia Centrali-Americana, Vol. IV, pt. 4, pp. 339-444.
- CHAMPLAIN, A. B., and KNULL, J. F.  
1921. Brief Notes on the Habits of North American Curculionids. Ent. News, Vol. 32, pp. 270-273.
- CHAPMAN, P. J.  
1938. The Plum Curculio as an Apple Pest. N. Y. State Agr. Exp. Sta., Geneva, Bull. 684. 75 pp.
- CHEVROLAT, A.  
1876. Curculionites Nouveaux de l'île de Porto Rico. Ann. Ent. Soc. France, 5th ser., Vol. VI.

- CHITTENDEN, F. H.  
1890. Notes on the Habits of Some Species of Rhynchophora. Ent. Amer., Vol. VI, pp. 167-172.  
1898. Biologic Note on *Conotrachelus elegans* Say. U. S. Div. Ent., Bull. 18, p. 94.  
1924. The Amaranth Curculio, *Conotrachelus seniculus* Lec. Journ. N. Y. Ent. Soc., Vol. 32, pp. 119-121.
- COOLEY, R. A.  
1922. Grasshoppers, Cutworms, and Other Insect Pests of 1921-1922. Mont. Agr. Exp. Sta., Bull. 150, p. 26.
- CROTCH, G. R.  
1873. Check List of Coleoptera North America. Salem.
- DEJEAN, P. F.  
1835-37. Catalogue des Coléoptères de la Collection de M. Le Baron Dejean. 2nd ed., 1835; 3rd ed., 1837. Paris.
- FABRICIUS, J. C.  
1801. Systema Eleutheratorum, Vol. II, pp. 1-687. Kiliae.
- FALL, H. C.  
1913. A Brief Review of Our Species of Magdalis with Notes and Descriptions of Other North American Rhynchophora. Trans. Amer. Ent. Soc., Vol. 39, No. 1, pp. 23-72.  
1917. New Coleoptera VII. Can. Ent., Vol. 49, pp. 385-391.  
1929. New Coleoptera VIII. Can. Ent., Vol. 61, pp. 54-59.
- FALL, H. C., and COCKERELL, T. D. A.  
1907. The Coleoptera of New Mexico. Trans. Amer. Ent. Soc., Vol. 33, pp. 145-272.
- FOLSOM, J. W.  
1936a. Notes on Little-Known Cotton Insects. Jour. Econ. Ent., Vol. 29, No. 2, pp. 283-285.  
1936b. Additional Notes on Little-Known Cotton Insects. Jour. Econ. Ent., Vol. 29, No. 6, pp. 1066-1068.
- GEMMINGER, M., and HAROLD, E.  
1871. Catalogus Coleoptorum, VIII, pp. 2181-2668. Munich.
- GERMAR, E. F.  
1824. Insectorum Species Novae. Hale.
- HAMILTON, J.  
1895. Catalogue of the Coleoptera of Southwestern Pennsylvania with Notes and Descriptions. Trans. Amer. Ent. Soc., Vol. 22, pp. 317-381.
- HENSHAW, S.  
1885. List of the Coleoptera of America, North of Mexico. Philadelphia.  
1895. Third Supplement to the List of Coleoptera of America, North of Mexico. Philadelphia.
- HERBST, J. F. W.  
1797. Kafer, Natursystem aller Insekten, VII. Berlin.
- HOPKINS, A. D.  
1921. Contributions toward a Monograph of the Bark Weevils of the Genus Pissodes. U.S.D.A. Bur. Ent., Tech. Ser., No. 20, pt. 1, pp. 1-68.
- HORN, G. H.  
1886. A Review of the Species Described by Oliver in the "Entomologie." Trans. Amer. Ent. Soc., Vol. 13, pp. 135-144.  
1895. Coleoptera of Baja California, Supplement I. Proc. Calif. Acad. Sci., Ser. 2, pp. 225-259.

- HUNTER, W. D., and PIERCE, W. D.  
1912. Mexican Cotton-Boll Weevil. U. S. Senate Doc. 305.
- HUSTACHE, A.  
1936. Curculionidae—Cryptorrhynchinae. In Junk's Coleopterorum Catalogus, Part 151, pp. 19-38.
- KASTON, B. J.  
1936. The Morphology of the Elm Bark Beetle *Hylurgopinus rufipes* (Eichhoff). Conn. Agr. Exp. Sta. Bull. 387, pp. 613-650.
- KLUG, J. C. F.  
1829. Preissverzeichniss vorräthiger Insecten-Doubletten des Königl. Zool. Museums, Berlin, p. 12.
- LACORDAIRE, T.  
1866. Genera des Coléoptères, VII. Paris.
- LECONTE, J. L., and HORN, G. H.  
1876. The Rhynchophora of America North of Mexico. Proc. Amer. Philos. Soc., Vol. 15, No. 96, pp. 1-455.
- LECONTE, J. L., and SCHWARZ, E. A.  
1878. The Coleoptera of Florida. Proc. Amer. Philos. Soc., Vol. 17, pp. 353-472.
- LENG, C. W.  
1920. Catalogue of Coleoptera of America, North of Mexico. Mt. Vernon, N. Y.
- LENG, C. W., and MUTCHLER, A. J.  
1933. Second and Third Supplements, 1925 to 1932, to Catalogue of Coleoptera of America, North of Mexico. Mt. Vernon, N. Y.
- MARSHALL, G.  
1932. Notes on the Hylobiinae. Ann. Mag. Nat. Hist., Vol. 9, pp. 341-355.
- MELSHHEIMER, F. E.  
1853. Catalogue Coleoptera United States. Revised by J. L. Leconte and S. S. Haldeman.
- MITCHELL, T. B.  
1936. A Revision of the Genus *Megachile* in the Nearctic Region, Part II. Trans. Amer. Ent. Soc., Vol. 61, pp. 1-205.
- MUTCHLER, A. J., and WEISS, H. B.  
1925. Beetles of the Genus *Conotrachelus* Known to Occur in New Jersey. N. J. State Dept. Agr., Bur. Statistics and Inspection, Circ. 87, pp. 3-22.
- NEAVE, S. A.  
1939. Nomenclator Zoologicus A-C. London.
- OLIVER, A. G.  
1807. Entomologie, Vol. V. 612 pp. Paris.
- PEAIRS, L. M.  
1941. Insect Pests of Farm, Garden, and Orchard. 4th ed., John Wiley and Sons, Inc., New York.
- PIERCE, W. D.  
1907a. On the Biologies of the Rhynchophora of North America. Studies Zool. Lab. Univ. Nebraska, No. 78.  
1907b. Contributions to the Knowledge of Rhynchophora. Ent. News, Vol. 18, No. 8, pp. 356-362.  
1908. A List of Parasites Known to Attack American Rhynchophora. Journ. Econ. Ent., Vol. 1, pp. 380-396.  
1916. Notes on the Habits of Weevils. Proc. Ent. Soc. Wash., Vol. 18, pp. 6-10.
- PROVANCHER, L.  
1877. Faune Ent. Canada, I, Coleoptera. 785 pp.

- QUAINTANCE, A. I., and JENNE, E. L.  
1912. The Plum Curculio. U.S.D.A. Bur. Ent. Bull. 103. 250 pp.
- SANDERSON, E. D.  
1904. Insects Mistaken for the Mexican Cotton Boll Weevil. Texas Agr. Exp. Sta. Bull. 74, pp. 3-13.
- SAY, T.  
1831. Descriptions of North American Curculionides, and an arrangement of some of our known species, agreeably to the method of Schönherr. New Harmony, Indiana. (Contained in "The Complete Writings of Thomas Say," in Entomology of N. A., Vol. I, ed. by J. L. Leconte. New York, 1859.)
- SCHAEFFER, C.  
1904. New Genera and Species Coleoptera. Journ. N. Y. Ent. Soc., Vol. 12, pp. 197-236.  
1906. New Rhynchophora. Can. Ent., Vol. 38, pp. 339-344.
- SCHÖNHERR, C. J.  
1837. Genera et Species Curculionidum, IV, pt. 1. Paris.  
1845. Genera et Species Curculionidum, VIII, pt. 2. Paris.
- SCHULZE, F. E., KUKENTHAL, W., and HEIDER, K.  
1929. Nomenclator Animalium Generum et Subgenerum. Berlin.
- SCUDDER, S. H.  
1882. Nomenclator Zoologicus. U.S.N.M. Bull. 19.
- SHARP, D.  
1918. Studies in Rhynchophora IV. A preliminary note on the male genitalia. Trans. Ent. Soc. London, Vol. 66, pp. 209-222.  
1920. Studies in Rhynchophora IX. The Sexes of *Conotrachelus brevisetis* Champ. Journ. N. Y. Ent. Soc., Vol. 28, pp. 74-78.
- SHARP, D., and MUIR, F.  
1912. The Comparative Anatomy of the Male Genital Tube in Coleoptera. Trans. Ent. Soc. London, Vol. 60, pp. 477-642.
- SHERBORN, C. D.  
1925. Index Animalium, C., pp. 945-1771.
- SLINGERLAND, M. V.  
1898. The Quince Curculio. Cornell Agr. Exp. Sta. Bull. 148, pp. 695-715.
- SLINGERLAND, M. V., and CROSBY, C. R.  
1930. Manual of Fruit Insects. Macmillan Co., New York.
- SNAPP, O. I.  
1930. Life History and Habits of the Plum Curculio in the Georgia Peach Belt. U.S.D.A. Tech. Bull. 188. 91 pp.
- SNODGRASS, R. E.  
1935. Principles of Insect Morphology. McGraw-Hill Book Co., New York. 667 pp.
- THOMSON, J. R.  
1932. Sex Differentiation of Adults of *C. nenuphar*. Journ. Econ. Ent., Vol. 25, pp. 807-810.
- ULKE, H.  
1902. A List of Beetles of the District of Columbia. Proc. U.S.N.M., Vol. 25, pp. 1-57.
- VAN DYKE, E. C.  
1930. New Rhynchophora (Coleoptera) from Western North America. Pan Pac. Ent., Vol. VI, No. 4, pp. 149-165.

- VERHOEFF, C.  
1896. Ueber das Abdomen des Scolytiden. Arch. f. Naturgesch., Vol. 62, pp. 109-144.
- WALSH, B. D.  
1864. References to Such Articles, Furnished by the Writer to Various Agricultural Journals, as Contain New Facts in Economic Entomology. Proc. Bost. Soc. Nat. Hist., Vol. 9, pp. 309-318.  
1868. First Annual Report on the Noxious Insects of the State of Illinois. 103 pp.
- WEISS, H. B., and DICKERSON, E. L.  
1919. Insects of the Swamp Rose Mallow, *Hibiscus moscheutos* L., in New Jersey. Journ. N. Y. Ent. Soc., Vol. 27, pp. 39-68.
- WELLHOUSE, W. H.  
1922. The Insect Fauna of the Genus *Crataegus*. Cornell Univ. Agr. Exp. Sta. Mem. 56.

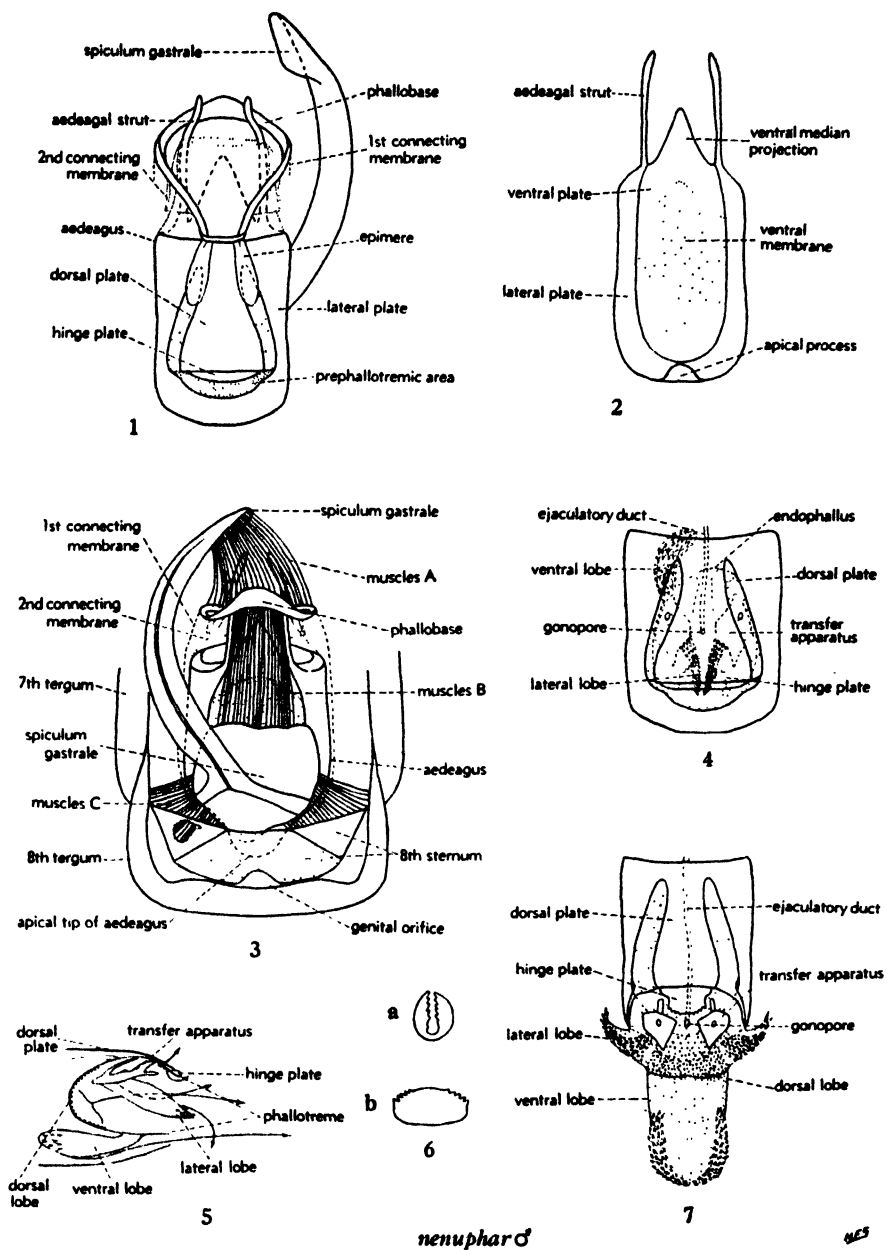
## PLATES

**NOTE:** In all of the genital illustrations excepting figures 4, 5, 7, and 11, the endophallus is not shown unless it projects into the prephallotremic area.

## PLATE I

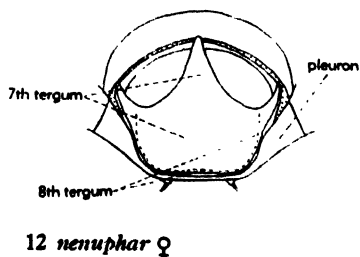
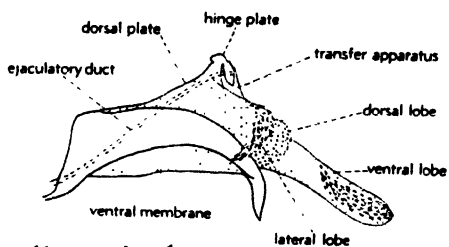
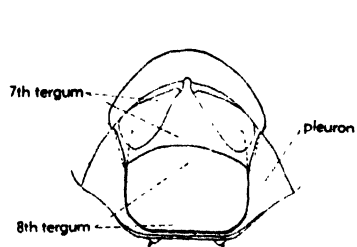
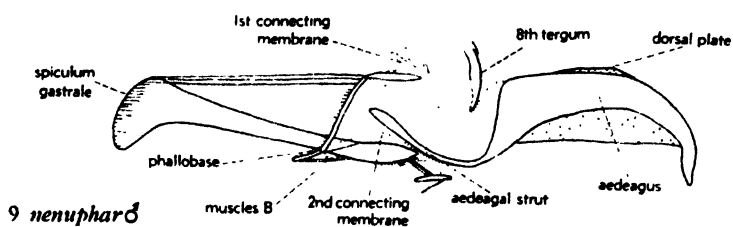
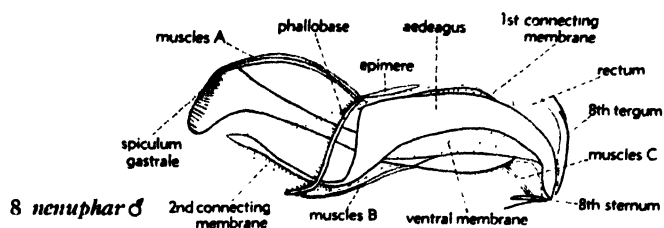
Male Genitalia of *C. nenuphar* (Hbst.)

- FIG. 1.—Dorsal view of phallus.  
FIG. 2.—Ventral view of aedeagus.  
FIG. 3.—Ventral view of phallus (slightly raised basally) within the body cavity.  
FIG. 4.—Dorsal view of aedeagus, showing endophallus in repose.  
FIG. 5.—Diagrammatic sketch of endophallus, showing the courses the various structures follow in the process of eversion.  
FIG. 6.—Diagrammatic cross-section of ventral lobe of endophallus, showing lobe in repose (a) and everted (b).  
FIG. 7.—Dorsal view of aedeagus, showing endophallus everted.



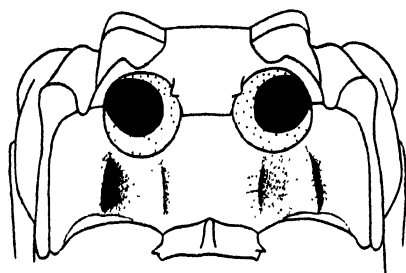
## PLATE II

- FIG. 8.—Lateral view of phallus within the body cavity, *nenuphar* (Hbst.).
- FIG. 9.—Lateral view of phallus, with aedeagus extruded from the body cavity, the endophallus in repose, *nenuphar* (Hbst.).
- FIG. 10.—Posterior view of male abdomen, showing visible eighth tergum, *nenuphar* (Hbst.).
- FIG. 11.—Lateral view of aedeagus, showing the endophallus everted, *nenuphar* (Hbst.).
- FIG. 12.—Posterior view of female abdomen, showing eighth tergum (dash line) concealed beneath seventh tergum, *nenuphar* (Hbst.).
- FIG. 13.—Ventral median section of phallobase, *juglandis* Lec., showing two types.
- FIG. 14.—Ventral median section of phallobase, *nivosus* Lec., showing two types.
- FIG. 15.—Ventral median section of phallobase, *elegans* (Say).
- FIG. 16.—Ventral median section of phallobase, *buchanani* n. sp., showing three types.
- FIG. 17.—Ventral median section of phallobase, *seniculus* Lec., showing three types.
- FIG. 18.—Ventral median section of phallobase, *aratus* (Germ.).

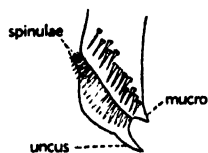


## PLATE III

- FIG. 19.—Ventral view of meso- and metathorax, *nenuphar* (Hbst.) ♂, showing the metasternal grooves from meso- to metacoxac.
- FIG. 20.—Anterior aspect of apex of mesotibia, *nenuphar* (Hbst.) ♀, showing uncus, mucro, and spinulae.
- FIG. 21.—Posterior view of male metauncus, *nenuphar* (Hbst.).
- FIG. 22.—Posterior view of male and female metaunci, *retentus* (Say).
- FIG. 23.—Posterior view of male metauncus, *hicoriae* n. sp.
- FIG. 24.—Posterior view of male and female metaunci, *affinis* Boh.
- FIG. 25.—Posterior view of male mesounci and metaunci, *elegans* (Say).
- FIG. 26.—Posterior view of male mesouncus and metaunci, *aratus* (Germ.).
- FIG. 27.—Posterior view of male metauncus, *tibialis* n. sp.
- FIG. 28.—Posterior view of male metauncus, *hayesi* n. sp.
- FIG. 29.—Mesoscutellum, *buchanani* n. sp., (a) dorsal aspect, (b) lateral aspect.
- FIG. 30.—Mesoscutellum, *albicinctus* Lec., (a) dorsal aspect, (b) lateral aspect.
- FIG. 31.—Anterior view of right protibia: (a) *tibialis* n. sp. ♂, (b) *aratus* (Germ.) ♂.
- FIG. 32.—Anteromedial view of left metatibia: (a) *anaglypticus* (Say) ♂, (b) *carolinensis* n. sp. ♂.



19 *nenuphar* ♂



20 *nenuphar* ♀



21 *nenuphar* ♂



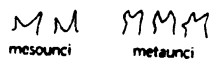
22 *retentus*



23 *hicoriae* ♂



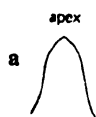
24 *affinis*



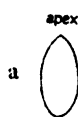
25 *elegans* ♂



26 *aratus* ♂



29 *buchanani*



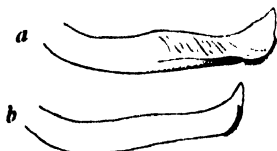
30 *albicinctus*



27 *tibialis* ♂



28 *hayesi* ♂



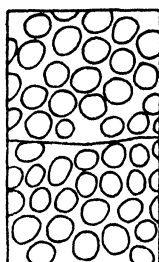
31 a *tibialis* ♂ b *aratus* ♂



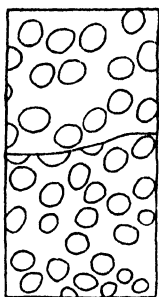
32 a *anaglypticus* ♂ b *carolinensis* ♂

## PLATE IV

- FIG. 33.—Punctures of first and second abdominal sterna, *elegans* (Say).  
FIG. 34.—Punctures of first and second abdominal sterna, *aratus* (Germ.).  
FIG. 35.—Lateral view of head and beak, *nenuphar* (Hbst.) ♀.  
FIG. 36.—Lateral view of head and basal portion of beak, (a) *affinis* Boh. ♀, and  
(b) *hicoriae* n. sp. ♀, showing relative distance between antennal scape  
and head capsule.  
FIG. 37.—Lateral view of head and beak, *hayesi* n. sp. ♂.  
FIG. 38.—Lateral view of head and beak, *aratus* (Germ.) ♂.  
FIG. 39.—Lateral view of head and beak, *elegans* (Say) ♀.  
FIG. 40.—Lateral view of head and beak, *hayesi* n. sp. ♀.  
FIG. 41.—Lateral view of head and beak, *aratus* (Germ.) ♀.



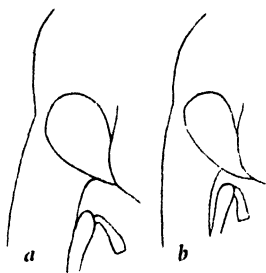
33 *elegans*



34 *aratus*



35 *nemuphar* ♀



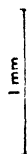
36 a *affinis* ♀ b *hicoriae* ♀



37 *hayesi* ♂



38 *aratus* ♂



425



39 *elegans* ♀



40 *hayesi* ♀



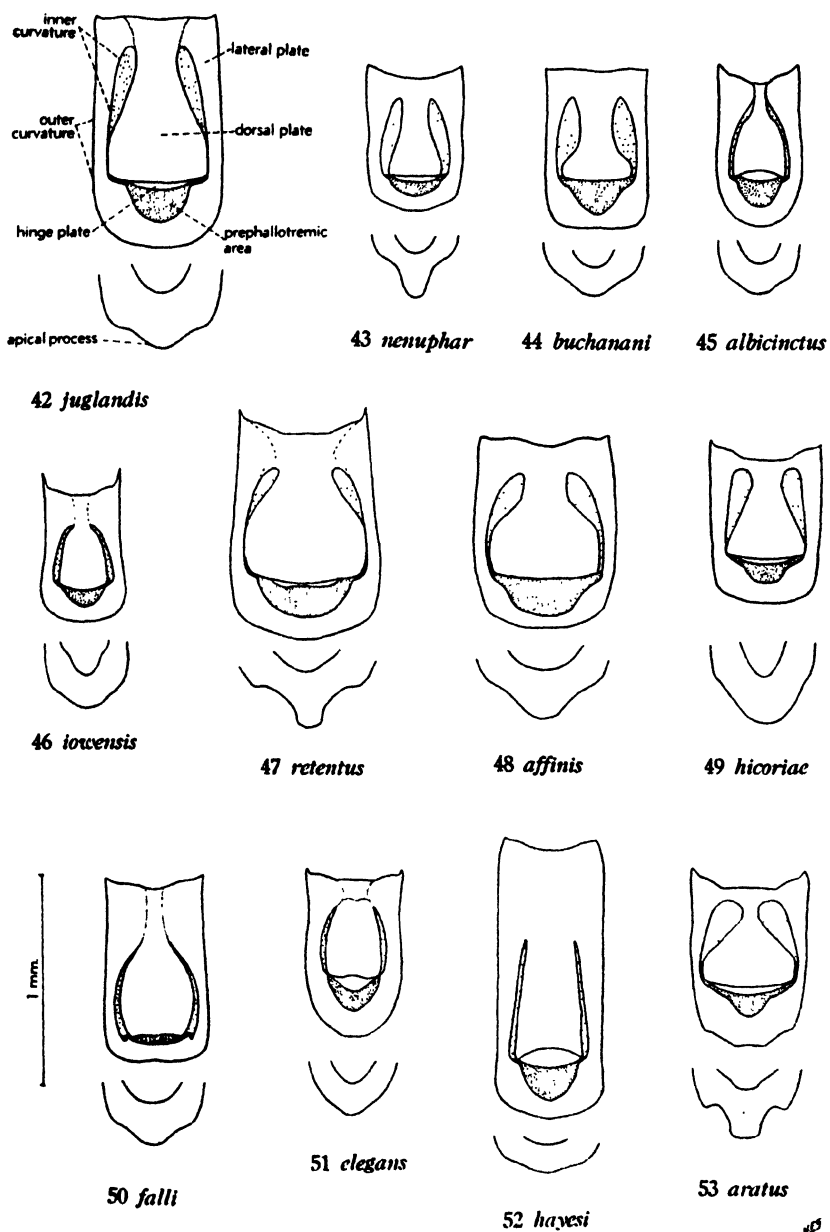
41 *aratus* ♀

## PLATE V

Dorsal View of Aedeagus  
(including separate sketch of apex)

FIG. 42.—*juglandis* Lec.  
FIG. 43.—*nenuphar* (Hbst.)  
FIG. 44.—*buchanani* n. sp.  
FIG. 45.—*albicinctus* Lec.  
FIG. 46.—*iowensis* n. sp.  
FIG. 47.—*retentus* (Say)

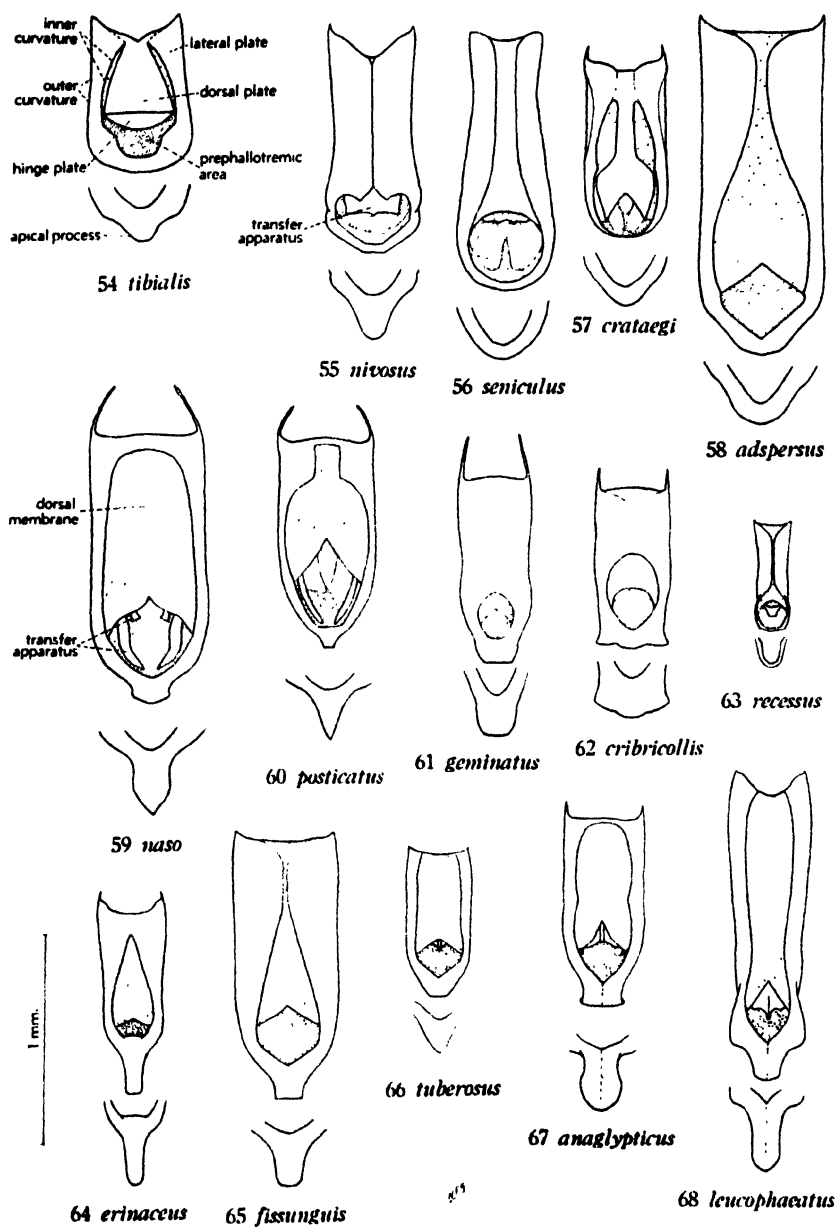
FIG. 48.—*affinis* Boh.  
FIG. 49.—*hicoriae* n. sp.  
FIG. 50.—*falli* Blatch.  
FIG. 51.—*elegans* (Say)  
FIG. 52.—*hayesi* n. sp.  
FIG. 53.—*aratus* (Germ.)



## PLATE VI

Dorsal View of Aedeagus  
(including separate sketch of apex)

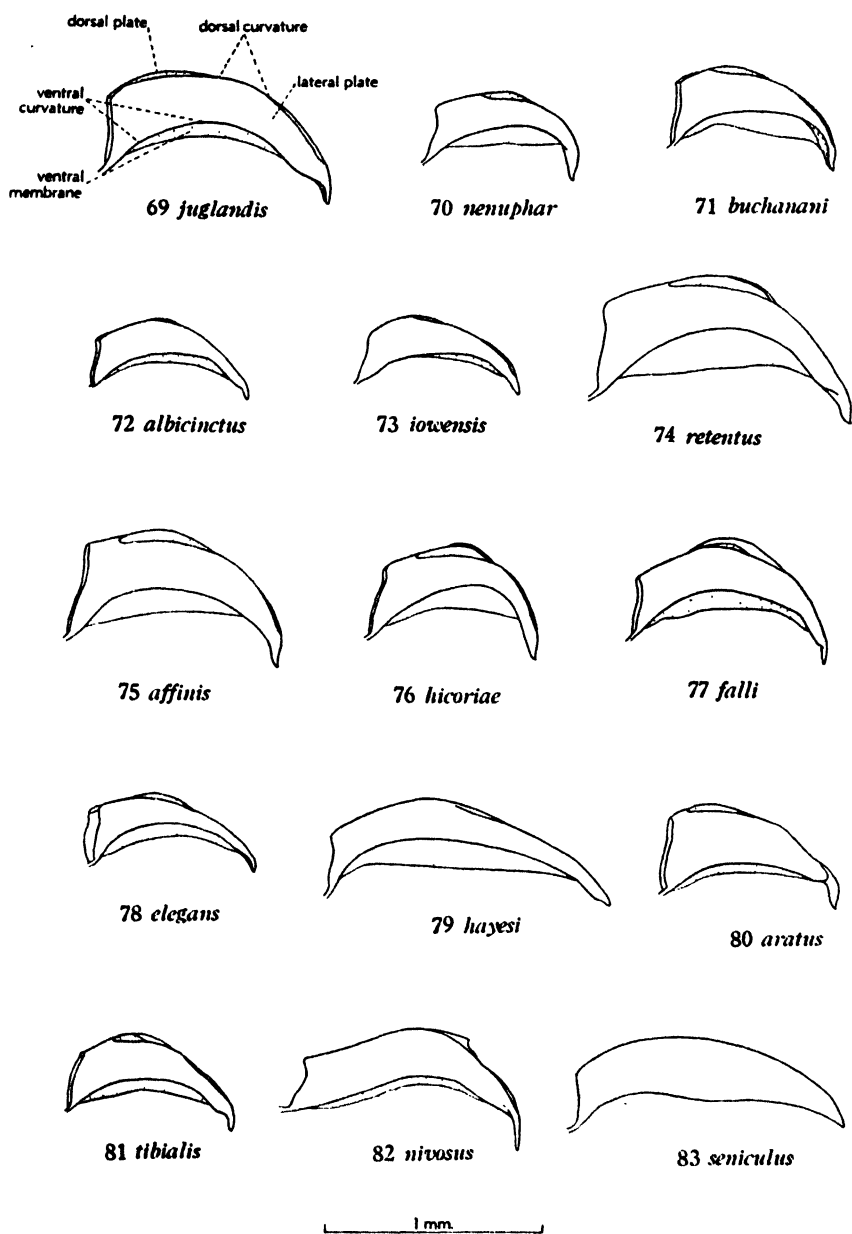
- |                                  |                                      |
|----------------------------------|--------------------------------------|
| FIG. 54.— <i>tibialis</i> n. sp. | FIG. 62.— <i>cribricollis</i> (Say)  |
| FIG. 55.— <i>nivosus</i> Lec.    | FIG. 63.— <i>recessus</i> (Csy.)     |
| FIG. 56.— <i>seniculus</i> Lec.  | FIG. 64.— <i>crinaceus</i> Lec.      |
| FIG. 57.— <i>crataegi</i> Walsh  | FIG. 65.— <i>fissunguis</i> Lec.     |
| FIG. 58.— <i>adspersus</i> Lec.  | FIG. 66.— <i>tuberosus</i> Lec.      |
| FIG. 59.— <i>naso</i> Lec.       | FIG. 67.— <i>anaglypticus</i> (Say)  |
| FIG. 60.— <i>posticatus</i> Boh. | FIG. 68.— <i>leucophaeatus</i> Fahr. |
| FIG. 61.— <i>geminatus</i> Lec.  |                                      |



## PLATE VII

## Lateral View of Aedeagus

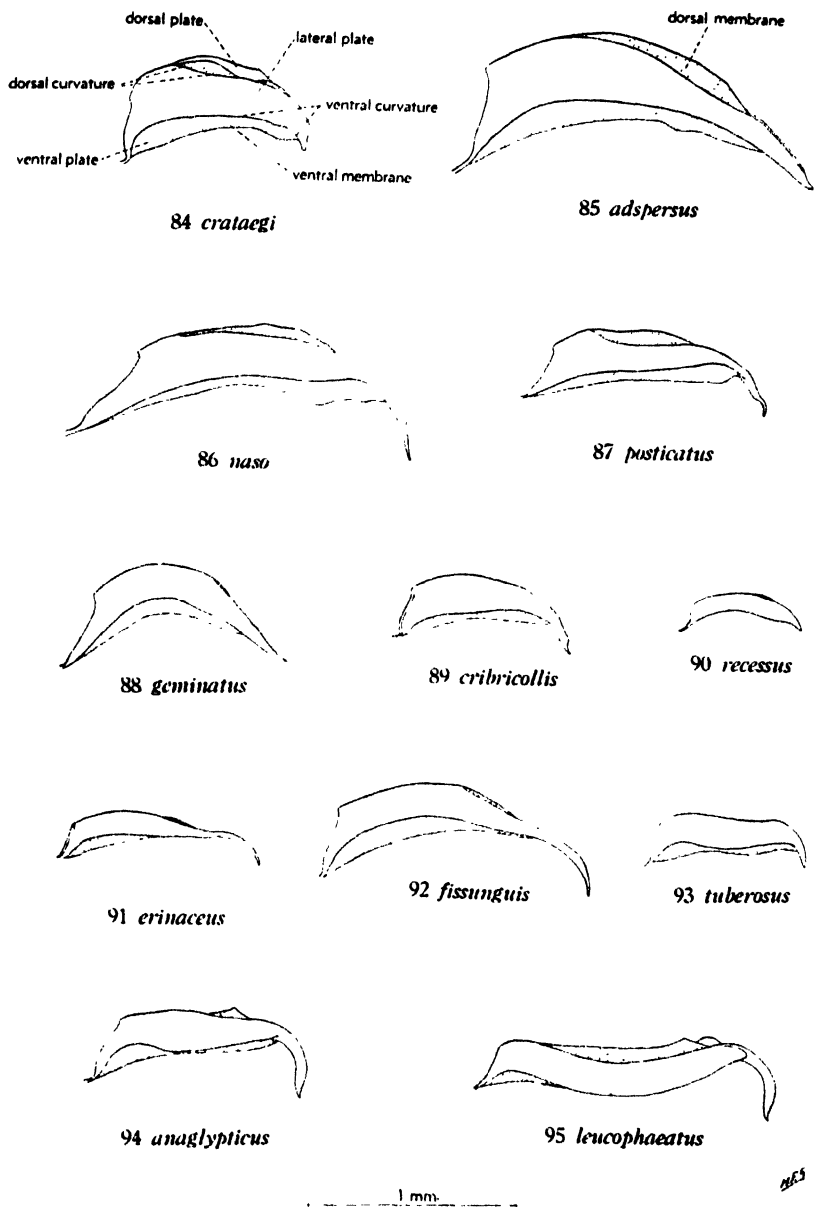
- |                                   |                                  |
|-----------------------------------|----------------------------------|
| FIG. 69.— <i>juglandis</i> Lec.   | FIG. 77.— <i>falli</i> Blatch.   |
| FIG. 70.— <i>nemuphar</i> (Hbst.) | FIG. 78.— <i>elegans</i> (Say)   |
| FIG. 71.— <i>buchanani</i> n. sp. | FIG. 79.— <i>hayesi</i> n. sp.   |
| FIG. 72.— <i>albicinctus</i> Lec. | FIG. 80.— <i>aratus</i> (Germ.)  |
| FIG. 73.— <i>iowensis</i> n. sp.  | FIG. 81.— <i>tibialis</i> n. sp. |
| FIG. 74.— <i>retentus</i> (Say)   | FIG. 82.— <i>nivosus</i> Lec.    |
| FIG. 75.— <i>affinis</i> Boh.     | FIG. 83.— <i>seniculus</i> Lec.  |
| FIG. 76.— <i>hicoriae</i> n. sp.  |                                  |



## PLATE VIII

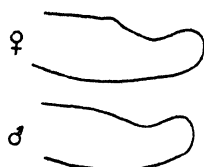
## Lateral View of Aedeagus

FIG. 84.—*crataegi* WalshFIG. 85.—*adpersus* Lec.FIG. 86.—*naso* Lec.FIG. 87.—*posticatus* Boh.FIG. 88.—*geminatus* Lec.FIG. 89.—*cribricollis* (Say)FIG. 90.—*recessus* (Csy.)FIG. 91.—*erinaceus* Lec.FIG. 92.—*fissunguis* Lec.FIG. 93.—*tuberosus* Lec.FIG. 94.—*anaglypticus* (Say)FIG. 95.—*leucophaeatus* Fahr.

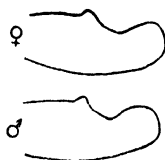


## PLATE IX

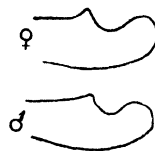
- FIG. 96.—Posterior view of apical portion of left profemur, *naso* Lec. ♂, ♀.  
FIG. 97.—Posterior view of apical portion of left profemur, *carinifer* Csy. ♂, ♀.  
FIG. 98.—Posterior view of apical portion of left profemur, *posticatus* Boh. ♂.  
FIG. 99.—Dorsal view of aedeagus, *carinifer* Csy., including a separate sketch of apical process.  
FIG. 100.—Dorsal view of aedeagus, *carolinensis* n. sp., including sketches of types of apical processes.  
FIG. 101.—Lateral view of head and beak, *carinifer* Csy. ♀.  
FIG. 102.—Lateral view of head and beak, *posticatus* Boh. ♀.  
FIG. 103.—Lateral view of aedeagus, *carinifer* Csy.  
FIG. 104.—Ventral view of a portion of aedeagus, *carolinensis* n. sp., to show relative length and position of the J-shaped and elongate bars of transfer apparatus; the loop of the J-shaped bar is directed toward the apex of the aedeagus.  
FIG. 105.—Lateral view of apical portion of beak, *carinifer* Csy. ♀, to illustrate distance (a) and distance (b).  
FIG. 106.—Lateral view of aedeagus, *carolinensis* n. sp.  
FIG. 107.—Ventral view of a portion of aedeagus, *anaglypticus* (Say), to show relative length and position of the J-shaped and elongate bars of transfer apparatus; the loop of the J-shaped bar is directed toward the apex of the aedeagus.  
FIG. 108.—Lateral view of apical portion of beak, *carinifer* Csy. ♂.  
FIG. 109.—Lateral view of apical portion of beak, *posticatus* Boh. ♂.



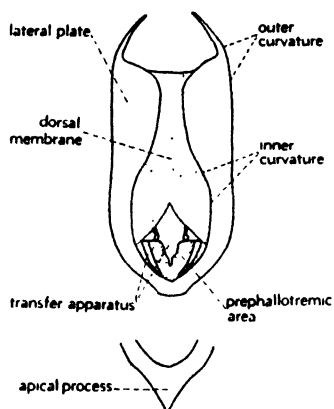
96 *naso*



97 *carinifer*



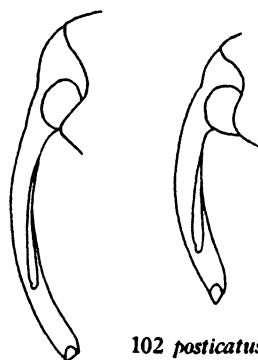
98 *posticatus*



99 *carinifer*

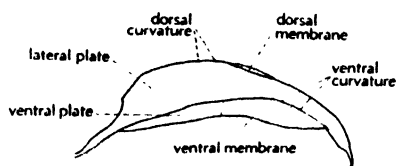


100 *carolinensis*

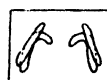


101 *carinifer*♀

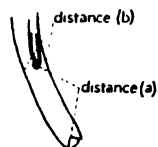
102 *posticatus*♀



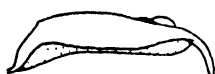
103 *carinifer*



104 *carolinensis*



105 *carinifer*♀



106 *carolinensis*



107 *anaglypticus*



108 *carinifer*♂



109 *posticatus*♂

1 mm.

MS



## INDEX

- adspersus* Lec., 94, 99  
*aedeagal struts*, 28, 36  
*aedeagus*, 27, 28, 29, 34, 35, 36, 37  
*affinis* Boh., 64, 65, 71, 130  
*albicinctus* Lec., 53, 54, 59, 130  
*alfalfa*, 79  
*Amaranthus*, 79, 128  
*anaglypticus* (Say), 10, 11, 118, 121, 126, 137, 140  
*antennae*, 18, 25  
*apple*, 50, 125  
*aratus* (Germ.), 11, 79, 83, 84, 85, 87, 88, 93  
*Argemone*, 128  
*argula* Fab., 48  
*aster*, 116, 136  
*atokanus* Fall, 11, 109, 111  
  
*Baptisia*, 136  
*beak*, 17, 25  
*bean*, 79  
*beech*, 125  
*Bidens*, 113  
*birch*, 125  
*blackberry*, 116  
*box elder*, 111  
*buchanani* n. sp., 48, 51, 55, 56, 59  
*butternut*, 46, 47, 63  
  
*Carex*, 113  
*carinifer* Csy., 104  
*carolinensis* n. sp., 137  
*Celtis*, 53, 56  
*cerasi* Peck, 48  
*Chaetochlorops*, 47, 63, 94  
*cherry*, 50  
*chestnut*, 125  
*Cholomyia*, 47, 63, 68, 94  
*cinctus* Van Dyke, 101, 104  
*Clematis*, 56  
*columbine*, 125  
*concentricus* (Oliv.), 37, 39  
*coronatus* Lec., 118  
*corn*, 128  
*cotton*, 79, 103, 116, 125, 128, 133, 135, 136, 140  
*cowpea*, 125  
*crataegi* Walsh, 96, 118  
*cribricollis* (Say), 11, 113, 114, 130  
*Cryptorhynchus*, 48, 60, 80, 88, 114, 121  
*Curculio*, 48  
*currant*, 50  
*Cyphorrhynchus*, 39  
  
*demens* Boh., 126  
*diaconitus* (Klug), 38, 39  
*dogwood*, 56, 103, 125  
*dorsal membrane*, 27, 28, 35, 36  
*dorsal plate*, 27, 28, 35, 36  
  
*Edesius*, 39  
*elegans* (Say), 11, 78, 79, 80, 87, 90, 91, 94, 116  
*elm*, 125  
*elytral costae*, 19, 20  
*endophallus*, 29, 30, 31, 32, 33, 34  
*erinaceus* Lec., 129, 130, 134  
*Euphorbia*, 128  
  
*falli* Blatch., 72  
*Fannia*, 63  
*femoral teeth*, 21  
*fissunguis* Lec., 129, 130, 131  
  
*geminatus* Lec., 111, 117, 130  
*genitalia*, 25, 33  
*Glycaria*, 39  
*gonopore*, 29, 30  
*gooseberry*, 50  
*grape*, 50  
*grass*, 79  
  
*hackberry*, 53, 56  
*hawthorn*, 99  
*hayesi* n. sp., 85  
*heartnut*, 46, 47  
*Hibiscus*, 133  
*hickory*, 47, 67, 71, 82, 83, 90, 93, 108, 109, 125  
*hickoriae* n. sp., 65, 67, 68, 69  
*hornbeam*, 125  
*huckleberry*, 50  
  
*integer* Csy., 104  
*internal sac*, 29  
*invadens* Fall, 101  
*iowensis* n. sp., 56, 57  
*irroratus* (Fab.), 37, 39  
  
*juglandis* Lec., 44  
*Juglans*, 46, 47, 62, 63  
  
*leucophaeatus* Fahr., 10, 76, 118, 126, 134, 140  
*Loeptes*, 11, 39, 109, 111  
*lucanus* Horn, 106  
  
*mallow*, 133  
*maple*, 125

- mesoscutellum, 19  
mesosternum, 19  
Metadexia, 47  
metasternal grooves, 24  
Microgaster, 68  
milkweed, 128  
mulberry, 125  
Myiophasia, 47, 68, 94, 126
- naso Lec., 94, 101, 109  
nectarine, 50  
nenuphar (Hbst.), 11, 48, 51, 59, 130  
nivosus Lec., 10, 73, 116, 130  
Notaris, 91
- oak, 103, 106, 108, 109, 111, 125, 128  
obesulus Hust., 118, 128, 129  
osage orange, 111
- peach, 50, 72, 99, 111, 116, 125, 140  
pear, 50, 99, 125  
Peridinetus, 39  
persimmon, 50  
phallobase, 27, 33  
phallus, 26  
Phylloxera, 83, 108, 109  
pigweed, 79, 128  
Pinus, 82, 116  
*plagiatus* Lec., 10, 73, 76  
plum, 50, 51, 83, 108, 125  
pokeweed, 116  
posticatus Boh., 10, 79, 94, 104, 106  
prothorax, 18, 19  
*puncticollis* Walsh, 113, 114, 117, 118
- Quercus, *see* oak.  
quince, 50, 98, 99, 103, 108, 109, 125
- ragweed, 113, 116  
recessus (Csy.), 11, 109  
retentus (Say), 11, 60, 68, 90, 116  
Rhynchaenus, 48  
*rubiginosus* Boh., 121  
Rubus, 136
- Salsola, 75  
seniculus Lec., 76, 84, 130  
serpentinus (Klug), 10, 38  
service berry, 125  
Sigalphus, 47  
sourwood, 125  
spiculum gastrale, 26, 27, 33  
spinach, 79  
strawberry, 50  
sulci, 17  
sunflower, 101
- tegmen, 27  
Thersilochus, 63, 126  
*tibialis* n. sp., 83, 91  
timothy, 136  
transfer apparatus, 30, 33  
Triaspis, 63, 68  
tuberosus Lec., 118, 119, 136  
tulip tree, 125  
tupelo, 125
- uncus, 21, 22, 24  
Urtica, 121
- Verbesina, 83
- walnut, 46, 47, 48, 62, 63





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# THE EMBRYOLOGY OF LARIX

WITH 86 FIGURES

BY

JAMES MORTON SCHOPF

CONTRIBUTION FROM THE DEPARTMENT OF BOTANY  
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## PREFACE

The earliest embryonic stage, because of the simplicity of its cellular makeup, is a logical starting point for developmental studies of plants. Evidence observed and deduced from embryological studies may be brought to bear on several fields of inquiry. Knowledge of the cellular sequence and mechanism by which the chain of heredity is transmitted to a new generation of plants should contribute to the success of undertakings in plant improvement, and this is particularly true with regard to gymnosperms. The embryonic stages consist of a series of "origins" of tissues and tissue complexes which necessarily condition the organization of the seedling and, less directly, that of the mature plant. The dynamic features of this sequence are especially important. Although the cellular organization of the gymnosperm embryo appears to be relatively simple, its physiology must be highly specialized. Unfortunately, experimentation with plant embryos is very difficult, and only during the last few years has a degree of success been achieved in this direction. Experimental studies were beyond the scope of the present investigation, but the histological details presented here may serve as a suitable background for such studies. The embryonic structures have been regarded from the standpoint of function, and their phylogenetic significance has been judged accordingly. It is realized that final proof of any phylogenetic hypothesis must be derived from phyto-paleontology, but only a small amount of fossil evidence can be brought to bear at present on gymnosperm embryology. Causal analysis of modern material should serve to identify with greater certainty those features denoting relationships due to common descent. Although conclusions based on such reasoning are still tentative, they may assist in revising the more formalized doctrines of interpretation.

The present study of the embryology of *Larix* was begun in 1932 at the suggestion of Professor J. T. Buchholz, and most of the material was presented in June, 1937, as a dissertation for the degree of Doctor of Philosophy in Botany at the University of Illinois. An abstract of the dissertation was published by the University in 1937. Some additional material was collected and sectioned in 1938, and a few recent bibliographical references have been added, but no new evidence has been found to alter the conclusions.

I wish to express my appreciation to Professor Buchholz for his guidance in conducting my research; his sympathetic discussion of the

many problems of interpretation has been of inestimable value. The assistance provided by my wife, Esther Julie Nissen Schopf, in the preparation of the manuscript and in many other ways, is mentioned as a matter of deserved record. I wish to express also my appreciation for the use of the photographic facilities of the Illinois State Geological Survey in preparation of the illustrations, and to Miss Meredith M. Calkins who assisted in completing the plates.

# CONTENTS

I. INTRODUCTION . . . . .	9
II. HISTORICAL ACCOUNT . . . . .	9
III. MATERIALS AND METHODS . . . . .	12
Killing and Fixation . . . . .	12
Embedding and Sectioning . . . . .	13
Stains and Staining . . . . .	13
IV. INVESTIGATION . . . . .	14
Embryo Development in the Pine Family . . . . .	14
Rate of Growth and Sequence of Embryo Development . . . . .	17
Development of the Gametophyte and Archegonium . . . . .	23
Fertilization. . . . .	26
The Early Embryo . . . . .	26
Pro-stage . . . . .	26
Meta-stage . . . . .	29
The Late Embryo . . . . .	40
Ana-stage . . . . .	40
Telo-stage . . . . .	50
The Gametophyte during Embryo Development . . . . .	57
V. DISCUSSION . . . . .	59
Relationship of Larix within the Pinaceae . . . . .	59
Tissues of the Larix Embryo . . . . .	60
The Apical Cell in Larix . . . . .	60
The Suspensor . . . . .	63
Tissues of the Mature Embryo . . . . .	65
The Primitive Spindle and Phylogeny . . . . .	68
Polarity and Polyembryony . . . . .	68
The Primitive Spindle Concept . . . . .	70
Application of the Spindle Concept to Gymnosperms . . . . .	72
Cycad and Conifer Types of Polyembryony . . . . .	76
VI. CONCLUSIONS . . . . .	80
BIBLIOGRAPHY . . . . .	82
PLATES . . . . .	85



## I. INTRODUCTION

Descriptions of the entire embryonal development are generally lacking for all conifers, and since little specific information about the embryology of *Larix* is available, there has been a need for a more comprehensive treatment. This study gives an account of the embryo of *Larix decidua* Mill, from the proembryo stage up to embryonic maturity. Some observations have also been made on *Larix laricina* (Du Roi) Koch, *Larix kaempferi* (Lamb) Sarg., and  $\times$  *Larix "eurolepis"* (*L. decidua* = *europaea*  $\times$  *leptolepis*). Origin of the various tissues present in the mature embryo, the detailed sequence of development up to this stage, and a theoretical interpretation of this embryogeny are presented.

The embryologic sequence shown by *Pinus* may be compared with *Larix* to great advantage, since they are both in the same family, and, in addition, the *Pinus* embryology is probably the best understood among all the conifers. The writer agrees with Doyle (1918) and others that *Larix* is more closely related to *Picea* and *Pseudotsuga* than to *Pinus*, but the embryonic sequence is not much better known in these other genera than it was in *Larix* when this study was begun.

Consideration has been given to the fundamental conceptions of embryology in terms of the embryonic development of *Larix*. Enough is known of embryo sporophytes throughout the plant kingdom at present to warrant broader theoretical consideration of the Pinaceous sequence of development. The "primitive spindle" concept of Bower and Lang is of particular interest in this connection.

## II. HISTORICAL ACCOUNT

Since the earlier literature on conifer embryology in general has been adequately reviewed by Buchholz (1918 et seq.), and since Schnarf (1933) in his recent compilation gives the present status of conifer embryology with considerable detail (especially the early stages), we need not dwell on the general background of the subject, but may proceed with a discussion of those few workers who have studied the embryology of *Larix*.

The paper by Geleznoff (1849) is the earliest significant contribution on the embryo of *Larix*, although Robert Brown (1843, 1844) had apparently observed polyembryony in *Larix* along with various other conifers as early as 1826. Geleznoff gives quite a complete series of stages up to slightly past the proembryo in a species which he never names, but was probably *Larix sibirica*, since this species is native in the vicinity of Moscow. His drawings may be taken as remarkably accurate for the period in which his work was done. However, since he was a strong advo-

cate of male inheritance as propounded by Schleiden and also strongly advocated by Schacht (1850), his interpretation of the fertilization stages was rejected long ago. Possibly his adherence to this misconception of fertilization caused the merits of his work to be overlooked by his more immediate successors. Strasburger does not mention this article in any of his publications on conifer embryology. Doyle (1925, 1926) has commented particularly on Geleznoff's correct and well-illustrated treatment of the pollination process in *Larix*. Aside from Hofmeister's (1850) review of Geleznoff's article, the work is very obscurely cited or omitted from the older literature. It is apparent that the concept of a cell as we know it today was not yet crystallized when Geleznoff made his drawings, but rosette cells are clearly shown with primary suspensors and four terminal embryonic cells. In the most advanced embryo system he shows the suspensor as longer than that shown in my figure 12, but the first division of the initial cells has not occurred.

Hofmeister (1862) gives a brief account of *Pinus larix*, which was probably *Larix decidua*, in the English translation of his "Vergleichende Untersuchungen." Although Hofmeister's general views have long since proved to be essentially correct, he does not give much specific information of value with reference to the present problem.

Strasburger produced in "Die Coniferen und die Gnetaceen" (1872) and in "Die Angiospermen und die Gymnospermen" (1879) the most monumental contribution of all early workers on gymnosperm embryology. Although he covered a large variety of conifers and did investigate *Larix* rather thoroughly in some particulars, chiefly relating to pollen development, pollination, and fertilization, he gives no details of embryonic development in this genus, and his neglect of the *Larix* embryo has been for the most part continued to the present. A great deal of present information on the embryos of conifers still depends in some measure on Strasburger's observations and figures. The figures of *Picea* embryos, which he gives in some detail, agree with *Larix* in most respects, and it is likely that the processes of embryogeny are very similar in both. Strasburger, however, did not obtain the critical stages during which the cells from one vertical row overgrow the other three to form the final embryo (as will be shown in the case of *Larix*), nor did he understand the autonomous embryonic potentialities of several proembryo cells.

Woycicki published in 1900 an account of the proembryo of *Larix*. This publication has not been available to the author, but in a paper published in 1923 he again illustrates *Larix* proembryos and mentions that these confirm his earlier observation, that the *Larix* proembryo is similar to that of *Pinus*.

Doyle started an investigation of the fruiting structures of *Larix* in 1917 and published (1918) an account of *Larix leptolepis*, which included

a detailed study of some abnormal pollen grains, and gave a brief account of the female gametophyte and proembryo. The final stage of embryonic development shown by him is a little later than that of Geleznoff. The similarity to *Pinus* is again pointed out.

In 1918 Buchholz published a most significant paper reporting his investigation of the early embryo of *Pinus*. Buchholz's recognition of the significance of the eight original cells of the early pine proembryo is the outstanding feature of this work inasmuch as it clearly defines the *primary units* of the embryology. The dissection technique, which he was the first to use effectively, made proof of his conclusions possible.

In 1920, 1926, 1929, and again in 1931, Buchholz briefly recorded the embryonic conditions in *Larix*, and recognized its similarity to *Pseudotsuga*, *Picea*, and *Abies*, all of which however were thought to be simple in their polyembryony.

Thus, while the early sequence in *Larix* was known approximately, the later stages up to the time of seed maturity, remained unknown. *Larix* is generally assumed to be similar to *Pinus* in later embryonic growth. However, many of the details of tissue development in *Pinus* are not yet described, so there is little repetition in the treatment of the later stages in *Larix*.

Buchholz and Old (1933) in their paper on the dormant embryo of *Cedrus* considered the histology of the mature embryo and illustrated one younger stage just prior to the initiation of cotyledons. For the first time the unique nature of the embryonic radicle in conifers was fully recognized. The structure surrounding the radicular plerome was named the *calyptroperiblem*.

Secretory elements which are to be described in the late embryo of *Larix* have also been reported from *Abies*, *Taxus*, and *Cedrus* by Chauveaud (1903a, 1903b, 1904). Buchholz and Old (1933) and Milhøne (1933) likewise found these structures in *Cedrus* and *Podocarpus*, respectively. In studies of seedlings, Hanes (1927) mentions "tannin sacs" in *Pseudolarix* and *Tsuga* and shows structures in *Sciadopitys* and *Araucaria* which are probably later developments from similar embryonic secretory elements. Notwithstanding the seeming widespread occurrence of these structures, little attention has been paid to them, and no mention of them may be found in current textbooks.

Bower in 1922 presented the "primitive spindle" concept. This generalization affords a unifying basis for comparison of the embryogeny of lower plants. In somewhat similar form, it is included in his book on "Primitive Land Plants" (1935). Lang is responsible in part for the chain of thought developed in this hypothesis, and it is expounded in a fundamental way, although not by that name, in his Manchester address to the British Association (1915). The basis of comparison afforded by this

hypothesis rests primarily on the conception of a fundamental organismal polarity and the manner in which early morphologic differentiation takes place. It seems desirable to extend these fundamental interpretations to higher plants, since the essential processes of embryology are comparable.

The genus *Larix* has been reworked taxonomically in recent years by Ostenfeld and Larsen (1930). The nomenclature used in the present study is in accord with their recommendations, except in quotations from other authors. Family and genus names are as given by Pilger (1926).

### III. MATERIALS AND METHODS

The University of Illinois Forest Tree Plantation provided most of the material for this study. The larch trees were started in 1870 by Professor T. J. Burrill and replanted in part in 1872 (see his report dated 1893). The grove now numbers about 200 good-sized trees, which ordinarily produce abundant cones. Of the two years during which collections were made for this investigation, 1933 was more fruitful than 1932. However, viable seeds were produced in both, and aside from the greater number of barren seeds in the first season and slightly later development of all stages, the embryos are quite comparable. There is no reason to believe that the embryogeny reported here is different from the normal sequence, although *Larix decidua* is not indigenous to this country.

*Larix laricina*, obtained near Grass Lake, Michigan, in 1934, was examined in late development of the early embryo. Slightly later stages of *Larix kaempferi* and *L. "eurolepis"* (a hybrid, either *L. europaea* (= *L. decidua*)  $\times$  *L. leptolepis* or its reciprocal), collected by Dr. Buchholz at the Arnold Arboretum, were also available.

#### KILLING AND FIXATION

Formalin acetic alcohol, as recommended by Chamberlain (1934), was used throughout this work, since it is suitable for preserving, as well as for killing and fixing. In general it was found to be quite satisfactory, although the dense archegonial cytoplasm shrank considerably when subjected to it. This seems to be a common defect, as scrutiny of the illustrations given by other authors shows, but even the details of pre-embryo organization are not necessarily obscured by it.

Cones of *Larix decidua* were gathered daily during the time fertilization was occurring in the spring of 1933. Later, collections were made every two or three days throughout development of the early embryo. Many collections were also made during the various stages of the late embryo. Numerous whole gametophytes were dissected out under a wide-field Greenough-type binocular microscope and placed directly into the

kill for later sectioning. To afford basis for the reliable interpretation of sections, many embryos were dissected from their gametophytes, stained in phloxine, and mounted in "diaphane," following the procedure originally devised by Buchholz (1918) and more fully described by him in a recent number of *Stain Technology* (1938).

#### EMBEDDING AND SECTIONING

Whole gametophytes were embedded by the customary xylol method, as given by Chamberlain (1934). In placing the material in the final paraffin block, eight or ten gametophytes were carefully arranged in rows side by side, as closely spaced and precisely parallel to one another as possible, each row being slightly shorter than the width of the cover slips which were to be used later. Each group was mounted as a unit on a wooden block, which was then clamped in the microtome, and longitudinal and transverse sections were cut 15 microns in thickness. This thickness is an economy in slides and in time; further, it is easier to reconstruct the details of histology from such sections than from thinner sections.

The early embryos are so small that it is necessary to section them within the gametophyte. Although they often are not axially aligned in relation to the gametophyte, this method of embedding and sectioning proved to be efficient. The chances for getting good sections by a single cutting operation are increased, and the possibility that parts of the work will be altogether fruitless is minimized, in spite of the fact that some lots of material consist predominately of sterile gametophytes which cannot be reliably detected before sectioning.

Some of the late embryos, and some which had been germinated, were dissected out of the gametophytes and embedded and sectioned individually.

#### STAINS AND STAINING

The stains used in this investigation were the safranin-picro-nigrosin combination recommended by Stover (1928), safranin and fast green, Haidenhain's iron alum with fast green, and Haidenhain's iron alum with orange III.

Stover's stain was used to a considerable extent, since it serves most purposes very well and is an exceedingly rapid technique once the timing is understood. The usual practice was to stain in 50% alcoholic safranin for two hours, run the slides through two steps to water, and rinse thoroughly. At this stage it was convenient to wipe off all the excess safranin adhering to the back and edges of the slide. The slide was then put in the half-and-half mixture of 1% picric acid and 1% nigrosin, both aqueous solutions. Time of staining varied greatly depending on the material; extremely meristematic tissue absorbed the stain much more

readily than mature tissue. For the embryo proper the time required for a good stain was about one minute. The slide was rinsed, the excess water being drained off, and was run very rapidly through a series of 25%, 50%, 75%, and 100% methyl alcohol. A mere dip into each of these alcoholic solutions is all that is necessary, as the safranin especially is very soluble in methyl alcohol. The next step was to half-and-half methyl alcohol and xylol, and then into pure xylol. The slide may be drained conveniently by touching the end on paper toweling between each step in the series. The slides were mounted in balsam in the usual way.

By this method the cytoplasm is stained a delicate lavender, with dark purple cell walls and a reddish purple nuclear differentiation. The nuclear membrane is quite distinct. Safranin is tenaciously held by fatty material, so that the megaspore membrane becomes brilliantly pink. Protein globules and starch grains both hold the safranin, the former being a vivid orange, and the latter tending to be yellowish, due probably to the picric acid. One of the very striking characteristics of this stain is the differentiation obtained in the germinating seedling, where the older tissues in process of elongation absorb more safranin than picro-nigrosin and the active meristems react oppositely. In the seven or eight years since many of the sections were made, there has been only a slight amount of fading.

The excellence of Haidenhain's iron alum for cytoplasmic and nuclear detail is very well known. This stain is better than the safranin combination for mitotic figures.

Fast green is a very useful stain, perhaps even better than the safranin combination for revealing cell walls of meristematic tissue. However, it tends to obscure materials in the cytoplasm which are so splendidly differentiated by the latter. Orange III is a weak counter-stain which does not seem especially applicable to this material. None of these stains are desirable for use individually.

## IV. INVESTIGATION

### EMBRYO DEVELOPMENT IN THE PINE FAMILY

So far as known, the proembryo is a relatively uniform structure in the Pinaceae, and at least some information is available for all nine genera, with the exception of *Keteleeria*. The embryologic sequence shown by *Pinus* is most completely known, and it is the best for general comparison. The purpose of this section is not only to pass in review the general embryologic sequence known for the Pinaceae, but also to introduce certain descriptive terms applicable to the detailed study of *Larix* embryos reported later on.

In pine, fertilization is followed by two free nuclear divisions of the

zygote. Free nuclear division of this sort is a unique characteristic of gymnosperms as a whole. The four free nuclei in the pine type of development then move to the base of the archegonium and come to rest in a single plane transverse to the archegonial axis. Each nucleus of this group soon divides to produce a new tier of nuclei above, and during this division, proembryo walls first form to enclose the four basal nuclei. The upper four nuclei still remain open to the archegonium above. The nuclei of the upper tier again divide, and the lower nuclei once again are enclosed by walls with four free nuclei above them. These free nuclei remain as they are, undergoing no further development. To distinguish them from the four free initial nuclei formed from the zygote, they are called the *relict nuclei*, since they have no function now but may have had in the past. Thus, a proembryo consisting essentially of twelve cells, eight walled and four relict nuclei, is formed. In *Pinus* each of the eight walled cells which are present at this stage of the embryogeny later develops an individual polarity of its own, and the four cells nearest the base of the archegonium, referred to hereafter as the *apical cells*, form potentially functional embryos; the tier of four cells directly above them forms rosette embryos. In *Larix* only the four lower cells (apical cells) of the proembryo manifest a definite polarity or show indication of embryo-forming capacity. The individualized growth of these cells in pine indicates very early that they are all potential embryonic cells. It is shown in the present study that each of the four apical cells in *Larix* is similarly potential. Since each of the four apical cells at the twelve-celled stage have individual polarity, these are designated as *polarity units*. A polarity unit is defined by applying the empirical test of observing its embryo-forming capacity. The first indication of polarity is evidenced by each of the apical cells dividing transversely, so that before the archegonium is ruptured by elongation there are three tiers of walled cells with a tier of relict nuclei above, sixteen in all. All the walled cells are similar in cytologic character at this time, but subsequent development shows that the new tier of cells, formed by segmentation of the four apical cells, are in no sense individual members but are organically subordinated to their respective apical cells. This is the tier of cells that elongate to become primary suspensors. Their elongation causes the four apical cells to break the wall of the archegonium and move out in contact with the undifferentiated gametophytic tissue. The proembryo is said to be complete just before the archegonium is broken, i.e., in the sixteen-celled stage. This intra-archegonial period of development represents a rather distinct chapter in the embryologic sequence and one which from various standpoints, physiological as well as morphological, can be compared with a considerable degree of accuracy among gymnospermous plants. In the subsequent discussion the period of proembryo development

has been shortened, for use as a term, and will be referred to as the *pro-stage*. The period beginning with the first elongation of the primary suspensor, and continuing through the period of great suspensor elongation, to the time when the embryo anlage becomes massive is termed the *meta-stage*. The pro-stage and the meta-stage together are taken to include the period of development of the early embryo.

The primary suspensor is a meta-stage embryonic organ present in all genera of the Pinaceae. When each of the four apical polarity units comes to function separately through cleavage, as they do soon after elongation of the primary suspensors in pine, the meristematic cell at the tip of each primary suspensor is clearly identified as a true apical cell. (See the definition of an apical cell on p. 60.) Cleavage does not take place with anything like the same definiteness in *Larix* as it does in pine. The polarity units remain united for the most part throughout meta-stage; nevertheless, the apical cells function toward the same end result and are just as definitely present. Meta-stage growth is chiefly by the addition of segments cut off by a transverse wall at the base of each apical cell and by subsequent successive elongation of each of these segments. Meanwhile, in pine, the rosette cells divide and each one forms a distinct embryo tip. The rosette embryos are always stunted but often grow for a considerable number of cell divisions, at which time they also possess a definite apical cell and more or less vacuolate cells behind. The rosette cells of *Larix* show none of these manifestations of polarity or growth but gradually degenerate. Thus we may say that the proembryo of *Pinus* contains eight demonstrable polarity units, whereas in *Larix* there are but four. *Cedrus* and *Tsuga* are known to resemble pine in having rosette embryos, and *Picea* and *Pseudotsuga* to resemble *Larix* (*Pseudotsuga* apparently even lacks rosette cells); *Abies* also is in this latter group. The embryologies of *Pseudolarix* and *Keteleeria* are less well known in this respect.

The manner in which the late embryo develops is inadequately known in the Pinaceae and among gymnosperms in general. It begins with formation of massive tissue originating from a tetrahedral apical cell both in *Pinus* and in *Larix*. Soon after massive apical tissue is formed a significant sequence of histogenesis begins. Cotyledonary tissues are the last formed of the several tissues which compose the mature embryo. Subsequent growth after cotyledon primordia are formed involves enlargement of the tissues already differentiated and observable.

It was convenient to divide the sequence of late embryo development into two stages, as in the sequence of early embryogeny. The period of histogenesis, beginning with formation of an undifferentiated mass of cells at the embryo tip after meta-stage development, and including the subsequent differentiation until cotyledonary primordia can be seen,

is termed *ana-stage*. *Telo-stage* development involves the subsequent increase in size leading up to embryonic maturation seen in the resting stage of the dormant embryo.

The sequence of histologic development in the late embryo has, up to now, not been followed closely for any gymnosperm. There are, however, numerous illustrations showing the structure of immature late embryos which have been briefly discussed by several authors. Nearly all these represent embryos in *telo-stage* development, which may be indicative of the generally rapid passage through the *ana-stages* of growth. Comparison of these illustrations with sections of *Larix* embryos shows that all the gymnosperms have similar tissues in their *telo-stage* development. However, significant variations appear to be present which may be due either to minor differences in the relative sequence of differentiation or differences in proportional development of particular tissues or both. Actually a highly complex sequence is involved, and the general similarity shown by late embryos of all gymnosperms is remarkable in view of the many other variations in embryogeny (in the *meta-stage* sequence particularly) which are already known. The histologic similarities between the late embryos of modern gymnosperms which are dissimilar in many vegetative and other characters surely represents a marked conservatism that suggests most strongly an ancient and monophyletic derivation for this division of the plant kingdom.

#### RATE OF GROWTH AND SEQUENCE OF EMBRYO DEVELOPMENT IN LARIX

Since precise comparison of the embryologic sequence with other gymnosperms, particularly in the late embryo, will involve variations chiefly of degree, an attempt has been made to represent the sequence diagrammatically for *Larix* in the chart on page 18. (The terminology used in this diagram is discussed below.) The structures characterizing the early sequence are entirely homologous with those known in pine (and also, as mentioned before, with other less known genera in the Pinaceae), but it is clear that the time required for completion of *meta-stage* growth varies considerably in these two genera, and it is quite likely that other members of the family also vary significantly.

In the material collected in 1933, it was observed that fertilization was taking place on the twentieth of May, and in some cases as late as the twenty-sixth, although at this later date, proembryo stages were predominant with some early *meta-stage* embryos present. Unfavorable environmental factors operating in 1932 were probably not only responsible for the preventing of abundant fertilization, but also for the retardation of the development of the embryos.

Organization of the proembryo following fertilization takes place

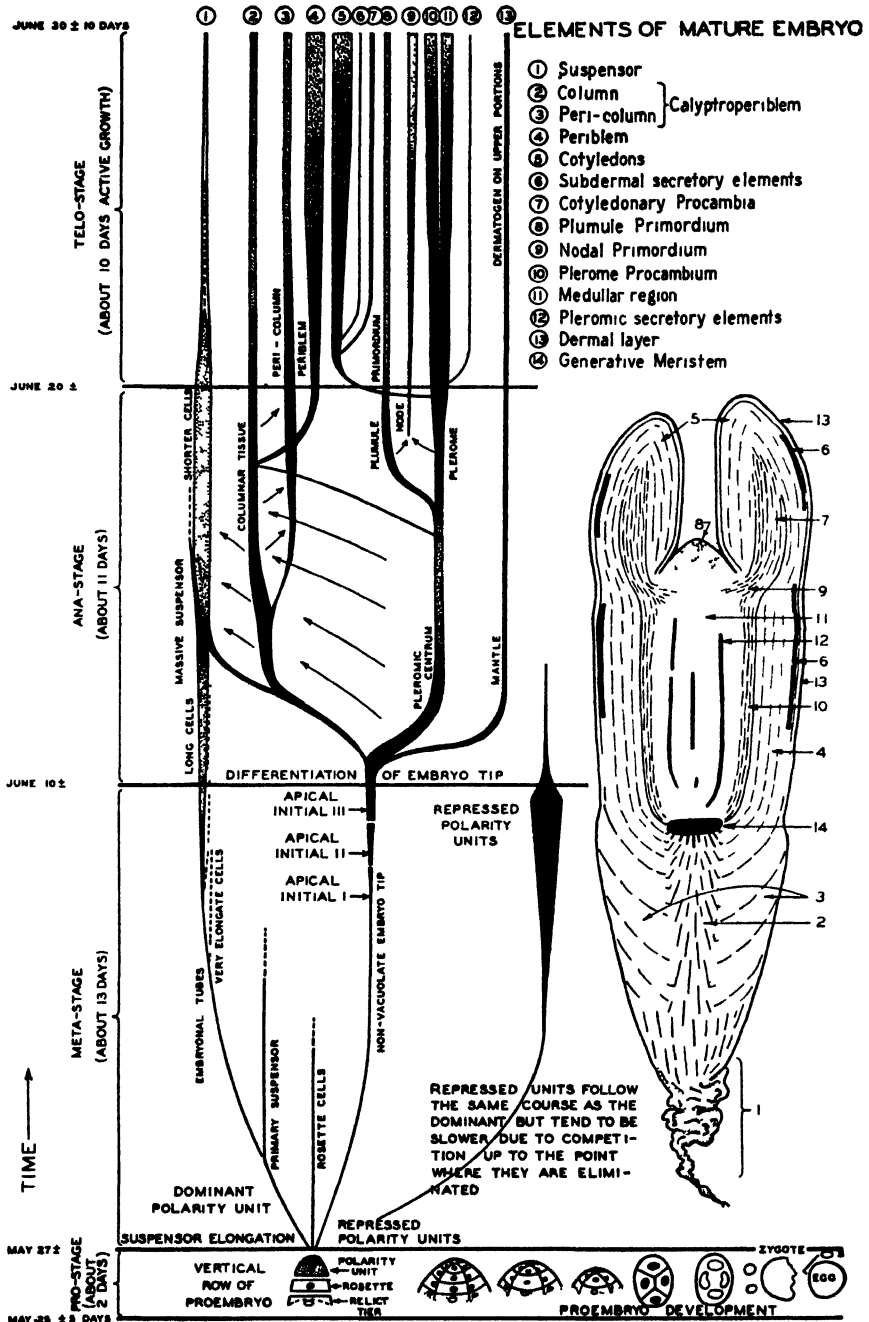


Chart showing embryologic sequence in *Larix decidua* Mill. Width of line indicates the relative tissue prominence, and density of shading indicates relative meristematic activity.

rapidly, so that the pro-stage is very short—probably much shorter than can be definitely ascertained by study of the collections. The length of time indicated by the diagram on the facing page may, therefore, represent variation in time of fertilization, as well as the period of pro-stage growth. Meta-stage development, on the other hand, takes about thirty-six per cent of the growth period in *Larix*, although in total number of cells and in mass, it represents less than one per cent of the total growth to maturity. Meta-stage in pine is of much briefer duration.

The contrast in time allotted to meta-stage development between *Larix* and pine is explicable by differences in their early embryogeny. Immediate cleavage of the four leading embryos of a single embryo system in pine removes the four polarity units from acute tactual competition with each other, and during meta-stage each one follows its course of development independently. The essentially hemispheric apical cell deviates from its early divisional sequence after formation of very few embryonal tubes (suspensor segments added subsequent to the primary suspensor segment), and generally after only one or two new unelongated segments have been formed. Then the next one or two segments in the series may be separated at an oblique angle, or the apical cell may merely cease division in a single plane abruptly, dividing subsequently in three different planes, the hemispheric apical cell thus becoming a tetrahedral initial. Further segmentation in pine results in formation of a massive tip of embryonic tissue.

In *Larix* all four polarity units remain closely associated through the meta-stage period. The four closely appressed apical cells cut off suspensor segments as in pine, but all the polarity units of the embryo system usually remain together until late meta-stage. Then one or more polarity units, depending on very slight superiorities in size and position instituted early in pro-stage, begin to cut off oblique segments in two planes away from the sides occupied by the other competitive apical cells. The additional cell mass thus built helps give the more advanced of the four polarity units added advantage and serves to separate the two-cutting-faced apical cell from the close association previously maintained with its neighbors. Frequently two of the apical cells are quite equally matched and form double rows of oblique segments nearly at the same time. After becoming separated at the apex one of the polarity units grows enough in advance of the others to relieve the spacial competition from that source, and in response to this release of tension separates a segment in the angle to partially overtop the other apical cells. Subsequent growth in *Larix* for a time duplicates that in pine after the tetrahedral apical cell is established there. The repressed polarity units in *Larix* are very quickly eliminated, since they are thrust back by direct contact with the basal elongating cells of the dominating unit. In essence the direct compe-

tition between polarity units of the same embryonic system is more acute in *Larix* than in *Pinus*, and this largely accounts for the longer meta-stage period of the former.

Early growth, as measured in terms of cell divisions, is probably relatively slow in both genera. Certainly mitotic figures are most infrequently seen during meta-stage. Physiologically the young embryo is undergoing adjustment, through the necessity newly arisen, of acquiring nourishment externally from the fluid filling the corrosion cavity instead of from more or less pre-adapted food material in the archegonium. The quantity of enzymes liberated also may influence rate of growth. In general an embryonic tip composed of few cells and lacking tissue specialization does not seem likely to be capable of functioning as efficiently and rapidly in early growth as later when it is more differentiated.

Assuming an equal rate of cell division it is probably safe to estimate that meta-stage is two to four times as long in *Larix* as it is in *Pinus*. It may be even longer because the approximation of the four apical cells of the system may very likely have a retarding effect on one another. One result of delay in meta-stage of *Larix* is that all early elongated suspensor segments are badly disintegrated, probably by enzymic activity. No doubt this factor has delayed interpretation of the early embryology of *Larix* considerably. In pine the suspensors are frequently well-preserved during meta-stage and even in early ana-stage (see Buchholz, 1918, Pl. IX, figs. 47-50), and this permits relatively easy and certain definition of polarity units and of embryo systems. In later meta-stage in *Larix* when the suspensor has disintegrated, the only positive clue to identification of embryo systems and polarity units is by observation of the apical cells. Since all but one dominant apical cell is eliminated in earliest ana-stage, adequate material and closely spaced collections are necessary if the sequence is to be followed.

During early ana-stage the growth rate jumps significantly, and the embryo may be said to enter upon its "grand period of growth." Ana-stage occupies about thirty-one per cent of the period of embryonic growth, and during this time the embryo undergoes a manifold increase in mass. The tetrahedral apical cell functions only for a short time to form a massive tip, which is somewhat smaller than that produced directly by a tetrahedral initial in pine before elimination.

Ana-stage is essentially the time of tissue origin, and with early elimination of the apical cell this progresses rapidly. First formed is the *columnar tissue*, composed of a large number of *derivation rows* (vertical series of cells which are each derived from a single initial)\* at the base

\*These are the units which constitute the rippenmeristeme of Schüepp (1926). Rippenmeristeme has been translated by Foster (1940, 1942) and others as rib meristem or as rib-like meristem. The writer believes that an English rendition as *costate meristem* for a tissue composed of derivation rows would be more suitable.

of the central mass of cells that later constitute the *plerome*. The alignment of derivation row initials at the base of the central mass (which is called the *pleromic centrum* at this stage) marks the origin of a new tissue zone between the *plerome* tip and suspensor. This tissue, while poorly defined at first, can be identified later as the *generative meristem* which gives rise to all the tissues of the primary root. Growth goes on rapidly with enlargement of both the columnar tissue and *pleromic centrum* which becomes essentially spherical in shape. The *pleromic centrum* continues to furnish cells to the tissue below, and these in turn furnish the lateral tissues of the embryo (*peri-column* and *periblem*). While lateral outgrowth is occurring below the centrum, apical prolongation takes place and a conical mass of cells is formed at the tip which are recognized as the *plumule primordium*. Two tissues originate primarily by outgrowth from the sides of the columnar tissue: (1) the *periblem* at the top, adjacent to the *pleromic centrum*, and (2) lateral "root-cap" tissue, designated as *peri-column*. The central columnar tissue becomes the "*säule*," or *column*, of the mature embryo.

The *peri-column* is the first lateral tissue, an outgrowth from the central column, and this is probably the largest single factor responsible for the notable increase in the diameter of the late embryo. To become *peri-columnar* tissue the more lateral cells of the column shift polarity abruptly and grow out obliquely upward and radially from the axis alignment. The *periblem* is a direct continuation of the *peri-columnar* tissue and is formed from it while the *plerome* is very short by the lateral introduction of *peri-columnar* cell rows growing out around the basal arc of the *pleromic centrum*. Consequently, at this early stage there is no difference between *peri-column* and *periblem*. The latter merely consists of the few upper layers of *peri-columnar* cells, which lie close enough to the *plerome* so that they are able to maintain intercalary growth parallel along its sides in later (chiefly *telo-stage*) development. The *periblem* cells and the very short *plerome* elongate together in *telo-stage*, with no further contribution from below.

Cotyledons are the last formed of the embryo tissue complement. They originate on the apical flanks of the *pleromic centrum* from cells comparable to the columnar row initials formed on the basal portion. Their origin is referable in part to the formation and lateral extension of procambial cells in the nodal region between the *pleromic centrum* and the *plumule primordium* and in part to the concurrent widening of the embryo caused by growth of the *periblem* tissue. When cotyledon primordia are formed, all the rudiments of the mature embryo are present and the *telo-stage* period is initiated. During *telo-stage* growth, which is of course directly continuous with that of late *ana-stage*, the greatest change is increase in size of the embryo organism. In this later develop-

ment the cotyledons and embryo axis grow considerably more in proportion than the *calyptroperiblem*, a term proposed by Buchholz and Old (1933) for the gymnospermic root cap which includes the column and peri-columnar tissues. This organ attains mature size sooner than tissues higher in the embryo. The axis increases in length by intercalary growth of the plerome and periblem of late ana-stage; the cotyledons are individually dominated by this same manner of growth, the chief effect being an increase in length. The increase in radial dimensions becomes progressively slower during telo-stage, and in later development it is due mostly to radial enlargement of cells already there rather than to new cell divisions. This is especially true of the periblem region. Procambial differentiation takes place first in the nodal region, then in the cotyledons as they grow, and along the margin of the plerome. The embryonal procambia are chiefly distinguished by the differences in proportional dimensions of the cells. The cells of the late embryo all remain in a meristematic condition until after germination, but during the growth sequence certain tissues in turn become considerably more meristematic than others.

A dermal layer is distinguishable over the embryo tip soon after it becomes massive, and it exists continuously thereafter. It probably is the food-assimilating organ during all the period of massive growth. Only in late telo-stage does it become sufficiently definite to be termed a *dermatogen* and then only upon the cotyledons and the adjacent surfaces of the axis. Before the formation of a definite *dermatogen* the dermal cover over the embryo is designated as the *mantle layer*.\* The mantle divides both anticlinally and periclinally as occasion demands. It is remarkable in its adaptability and efficiency in maintaining a smooth symmetrical surface contour over the embryo during all stages of late embryonic growth.

During telo-stage the embryo becomes equipped with a peculiar system of secretory elements which are not to be confused with resiniferous passages arising later in the seedling. One group of the secretory elements arises in the central part of the plerome and finally extends up into the cotyledonary procambial areas. Others are formed sub-dermally in the periblem and adjacent to outer surfaces of the cotyledons. They do not intercommunicate and their function is unknown, but because of their chromophilic contents they are prominent in late telo-stage. Active telo-stage development, taken to represent the period of growth after all

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\*Schmidt (1924) has called the more or less regular investing cell layers of mature shoot apices "*tunics*." The term "*mantle*" is preferred here because it seems desirable to distinguish the embryonal from the mature meristematic layer or layers. The mantle probably is active as an agency for food transfer in the embryo and seems less definite histologically than a tunic, except possibly in the region of the telo-stage shoot primordium. The plumule mantle precedes formation of any dermatogen—the outermost tunic layer may be considered, in part at least, a juvenile differentiation of dermatogen in histologic continuity with it. Foster (1942, pp. 22-24) has recently discussed the significance of the tunica.

tissues of the mature embryo may be recognized, occupies about twenty-eight per cent of the active growth period. By the end of June the embryo is essentially mature, although it is not likely that enlargement stops altogether until later in the summer.

The origin of later tissues of the embryo from pre-existent tissues, the relative prominence of the various tissues in the embryo at any particular stage of development, the relative meristematic activity of the tissues, and the approximate time period of their existence during the embryologic sequence have been indicated diagrammatically in the chart on p. 18. The tissues of the late telo-stage embryo are indicated on the accompanying embryo diagram, the key numbers corresponding for both the embryo diagram and the telo-stage development on the chart. The density of shading indicates the estimated relative meristematic activity of the different tissues at any stage of their development. All except the matured and collapsed cells of the suspensor are meristematic, inasmuch as they are all capable of division, but there are important differences in the rates at which cell division normally occurs in the tissues, and it is this feature which is approximately indicated. Similarly an attempt to evaluate the apparent relative prominence of the tissues through the embryologic sequence is indicated by the widths of lines employed. Obviously both meristematic activity and the prominence of the various tissues permit no accurate measurement by ordinary histologic methods, but if this is kept in mind the diagram may give a more accurate picture of the developmental sequence as a connected and absolutely interrelated phenomenon than is possible by means of description alone.

#### DEVELOPMENT OF THE GAMETOPHYTE AND ARCHEGONIUM

The gametophyte agrees in its early development with the usual Pinaceous sequence. Recently Saxton (1930) found that hypodermal derivation of the linear tetrad, reported by Strasburger (1879) is not an ordinary occurrence, but that in *Larix europaea* (= *decidua*) the tetrad is formed deeper in the nucellus. Sections of cones showing early gametophyte stages were prepared, which tend to support Saxton's statement, although none were at a stage early enough to show the original tetrad.

The gametophyte passes through the characteristic free nuclear stage and, with the formation of cells, differentiates archegonium initials at the micropylar end.

The number of archegonia varies from one to five in the material examined, three or four being the usual number. Doyle (1918) reports that the archegonia in *Larix leptolepis* are always five in number. The variable number as found in *L. decidua* is more typical for the *Pinaceae*.

The archegonia are always enclosed by a separate layer of jacket cells even when they are close together and the jacket layers somewhat com-

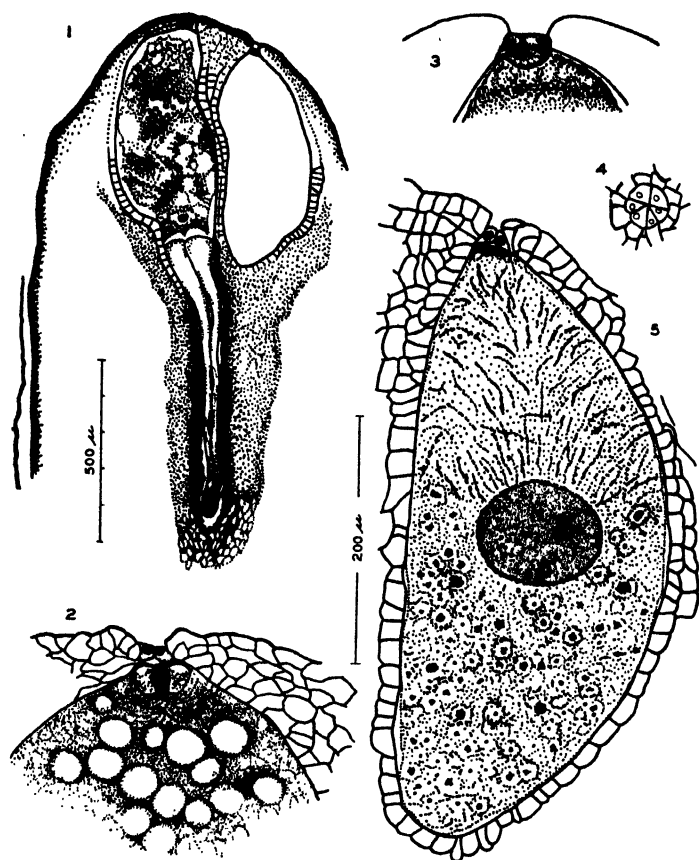


Fig. 1.—Longitudinal section of an early meta-stage embryo system within the gametophyte. Stippled area corresponds with the central cone of more opaque tissue. Collection of May 26, 1933.

Fig. 2.—Longitudinal section showing division of the central cell at the apex of an archegonium. Collection of May 21, 1933.

Fig. 3.—Section similar to Fig. 2 and from the same collection, showing ventral canal cell.

Fig. 4.—Transverse section of neck of archegonium.

Fig. 5.—Longitudinal section of archegonium just prior to penetration of pollen tube. (The pollen tube has traversed the nucellus tissue above this archegonium.) Collection of May 30, 1933. (Figs. 2-5 drawn at the same magnification.)

pressed (Figs. 5, 48, 49, 51, and 52). Doyle states that the jacket may be reduced to a single layer or be altogether absent in *L. leptolepis* where the archegonia are crowded. The jacket cells are smaller and more uniform in shape, with considerably denser cytoplasm than the gametophytic cells surrounding them. The neck of the archegonium is never more than one cell deep. The neck cells are variable in number, however, from four to eight. Figs. 2, 3, 4, and 5 show typical examples. Quadrant walls are formed by equal anticlinal segmentation of the original neck initial, and these four cells may or may not be subdivided as the two shown in Fig. 4. Doyle mentions the shallow archegonial chamber in *Larix leptolepis*. In fertile archegonia of *Larix decidua* a similar condition is found. However, the neck cells of archegonia long past fertilization appear sunken into the gametophyte because a rather long canal is formed by tissue growing up around them.

Doyle and his co-workers (1925, 1926, 1935) have studied the pollination processes of *Larix* quite thoroughly. There is little that can now be added to their account. It is still unexplained exactly how the pollen is transferred from the stigmatic flap to the nucellus. However, this transfer does occur and abundant pollination results, often with the several archegonia being fertilized at about the same time. The four archegonia shown in Fig. 52 have all been fertilized, essentially simultaneously. Two empty pollen grains and the pollen tubes leading from them directly through the nucellus are shown in Fig. 48. Here also both archegonia have been fertilized. In this instance the nucellus has been slightly dislodged from its position next to the gametophyte in the process of dissection and paraffin embedding, so that the termination of the pollen tubes cannot be followed.

The nucellar tip on which the pollen grains rest is truncated. In dissections this tip area is clearly visible, since it results from collapse of the original nucellar-tip cells with consequent brownish discoloration.

The archegonial cytoplasm is light-staining and frothy, with numerous large clear vacuoles prior to formation of the egg nucleus. This condition is shown in Fig. 2 as the ventral canal cell is being produced. Later, after formation of the ventral canal cell (shown in Fig. 3, and a later stage in Fig. 5), the clear vacuoles disappear and the cytoplasm becomes more chromophilic. The egg nucleus enlarges greatly to about  $300\ \mu$  in diameter, and meanwhile the ventral canal cell disintegrates. Just prior to fertilization the archegonial cytoplasm becomes exceedingly fibrillar, especially in the upper part and around the egg nucleus. The basal portion is commonly full of deeply-staining granules and globules (Hofmeister bodies) of various sizes. This condition is shown in Fig. 5 and also in transverse section of four archegonia in Fig. 51. In the latter case the fibrils form a definitely spiral pattern throughout the upper part of

the archegonium. They may have a definite part in the process of fertilization not now understood. Lawson (1909, Pl. XIII, figs. 26 and 27) shows fibrillae in archegonia of *Pseudotsuga* at about this same stage, although it is not certain that they are spiral as in *Larix*.

#### FERTILIZATION

Details of the entrance of the pollen tube into the archegonium are not known. The discharge vacuoles at the top of the archegonium, as mentioned by Chamberlain (1935, p. 334), are visible for some time after penetration by the male nucleus, until fertilization is complete. Only one archegonium was found in which the two gametic nuclei were still separate, so that fertilization appears to take place quite rapidly.

The egg nucleus is very large at this time. After fusion of the two nuclei, the upper surface of the nuclear membrane becomes quite irregular, as seen in Fig. 52, and it sometimes becomes extremely invaginate. The zygotic nucleus becomes elongated during the first mitosis. The spindle seems to lie entirely within the nuclear membrane, with no apparent segregation of male and female chromosomes. The stain used was not suitable for cytological study at high magnification, however, and consequently the fine details of chromosomal behavior cannot be reported. There is no definite orientation of this first spindle; sometimes it is transverse and in other cases oriented lengthwise of the archegonium.

At the end of two free nuclear divisions the four free proembryo nuclei are found at the base of the archegonium as shown in Figs. 53 and 54. As in *Pinus*, the first walls of the proembryo are formed during the next nuclear division. The free nuclei resulting from division of the zygote are very much smaller in size. (Compare the free nuclei shown in Fig. 53 with the fusion nuclei in Fig. 52, or the gametic nucleus in Fig. 51, all of which are reproduced at the same magnification.)

The so-called "Hofmeister bodies," or protein globules, found in the archegonium during fertilization and for some time afterward, were for a long time considered as separate nuclei by the early workers. They are most abundant in *Larix* succeeding fertilization and persist for a considerable time until after elongation of the suspensor. No doubt, they constitute part of the food which nourishes the proembryo. It is easy to understand how they came to be confused with nuclei, because it is often very difficult to distinguish them from the relict nuclei in the later proembryo stages.

#### THE EARLY EMBRYO

*Pro-stage*.—From the time of fertilization to the beginning of elongation of the suspensor, the embryo is considered to be in the pro-stage. The proembryo of *Larix* has been studied by Woycicki (1900, 1923) and

Doyle (1918), who stated that its development is essentially similar to that of *Pinus*. The present study also confirms this.

As in *Pinus*, the proembryo of *Larix* is derived from the four first-formed free nuclei. Polarity units originate from each of the four cells at the base of the archegonium in the eighth nucleate stage. Each of the four basal cells divide to form the primary suspensor cell above, and the apical initial below. The upper four cells of the eight-celled proembryo divide prior to this first division of the polarity units below, to form the rosette cells and the tier of relict nuclei. Thus each vertical row of the proembryo finally formed in *Larix* consists of an apical initial cell, a primary suspensor cell (both of which are functionally connected and constitute a polarity unit), a rosette cell which exhibits no special attributes of polarity, and above this the relict nucleus in a cell open on top into the archegonium.

Chamberlain, in his recent book on gymnosperms (1935, p. 347), states that the four tiers of cells in *Pinus* are "almost geometrical in their symmetry." This is not the case in *Larix*, as is shown by transverse sections of the proembryo. The symmetry both in *Larix* and in other genera is less exact than might be inferred from the literature. In the first place, the archegonium is not perfectly cylindrical in shape but generally broadly elliptical, with the longer of its transverse axes placed radially within the gametophyte. When the free nuclei move to the base of the archegonium, mutual repulsion leads them to assume a balanced position in which there are two nuclei occupying the narrower poles of the ellipse, and two occupying the opposite broader sides. When walls are formed these latter two are seen to adjoin one another for a short distance by a straight central wall. The cells formed on the narrower poles of the ellipse abut on this short central wall by a sharp angle. Sometimes spores derived from an oval pollen mother cell assume this same configuration after simultaneous division. (See Wodehouse, 1929, who discusses the configurations of pollen grains.) It is believed that similar factors of nuclear repulsion are causes for both. This proembryo condition, where two vertical rows on opposite sides adjoin by a straight central wall segment, with the other two vertical rows on the narrower extremities of the ellipse not mutually adjoining, is called a *tetragonal* arrangement. This arrangement is well illustrated by the transverse section of a proembryo tip seen in one archegonium in Fig. 50 (less notably in the other), and it is also seen in Fig. 8. What has actually happened is that the two central nuclei have been able to claim for themselves a larger portion of space at the base of the archegonium than their neighbors on the narrower poles of the ellipse. The central wall segment is variable in width, varying with the original amount of asymmetry in the archegonium. Practically all proembryos have been found thus asymmetric in their original

construction to a greater or less degree. In later growth the slight initial advantage for the larger cells becomes increasingly important with reference to selection of the single successful polarity unit.

The shape of the archegonial base not only has a considerable influence on the positions of the vertical walls of the proembryo but also on the transverse walls. These are not formed at right angles to the vertical axis of the archegonium but incline downward from the center to intersect the sides at lower levels. Thus, if the archegonium and vertical rows approximated ideal *radial* symmetry, the apical cells (lowest tier) of each vertical row would be essentially tetrahedral in form, with one outer side slightly rounded to conform with the basal archegonium wall. As isodiametric an apical cell as possible would be formed. The downward slope of the transverse walls is diagrammatically drawn in Fig. 6 according to this ideal specification. Since only two apical cells (the smaller ones) have a single corner nearest the archegonium center, only these cells approximate the ideal form. The two rows abutting by a straight central wall conform to the shape of the former in that their transverse walls incline downwards from the center, but due to their added width they are more accurately described as asymmetrically wedge-

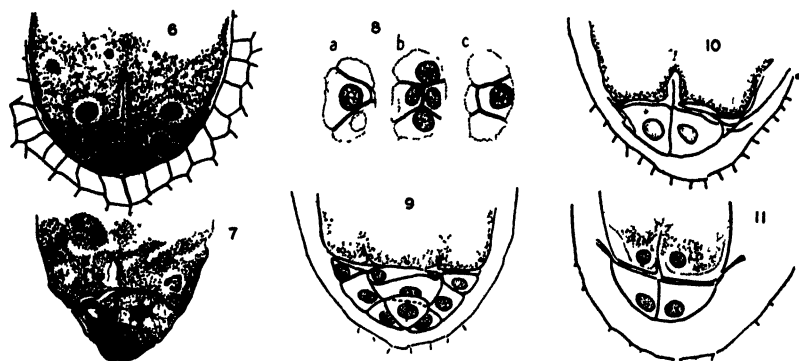


Fig. 6.—Diagrammatic drawing of proembryo in twelve-nucleate stage (8 completely walled cells, 4 open above; only half the total number are shown).

Fig. 7.—Longitudinal section of proembryo in same stage as preceding figure. Magnified about 150 times. Collection of May 26, 1933.

Fig. 8.—Oblique cross section of proembryo in eight-nucleate stage. Note the arrangement of cells in *b*, characteristic of proembryos formed in elliptical archegonia. Magnified about 140 times. Same collection as Fig. 7.

Fig. 9.—Drawing of proembryo reconstructed from several serial sections. Magnified about 175 times. Same collection as Fig. 7.

Figs. 10 and 11.—Longitudinal sections of proembryos at about the same stage as shown in Fig. 8. In both cases the sections are slightly oblique with reference to the archegonial axis. On this account the base of the archegonium appears broader and transverse walls of the proembryo do not show their true obliquity. Magnified about 175 times. Same collections as Fig. 7.

shaped. The appearance of these apical cells, as shown at the base of the archegonium, is best seen in Fig. 8b. Fig. 9, drawn from serial sections, represents a later stage in which the apical cell has divided (as in Fig. 6) to complete the proembryo.

Figs. 10 and 11 are earlier stages which do not show the true relations of the transverse walls due to obliquity of the section across the end of the archegonium. These show the most prevalent appearance of individual sections. It is impossible to orient definitely the material to show more suitable longitudinal sections of proembryos; but if a sufficient number of sections are made, some of them can be easily interpreted; the majority are obliquely cut across the planes of symmetry. Transverse sections are more satisfactory. Fig. 49 shows a section containing two twelve-celled proembryos in which the obliquity of the transverse walls is clear. In both cases cells and nuclei of the upper tier are shown peripherally toward the circumference of the archegonium; toward the center the inclined transverse wall is crossed, and within this is part of the next lower tier with its nuclei. Thus, it is demonstrable that the transverse walls of the proembryo slope downward away from the center to a considerable degree, forming in this way an obtuse angle with the basal and outer wall of the archegonium. The transverse wall of the highest (rosette) tier is much less sloping than that covering the basal (apical cell) tier. The figures of a *Pseudotsuga* proembryo given by Lawson (1909, Pl. XIV, fig. 40), although incomplete, show the transverse walls to be similarly sloping and also suggest strongly that the vertical rows are dissimilar just as in *Larix*.

*Meta-stage*.—The meta-stage is begun at the time of elongation of the primary suspensors. The four polarity units elongate coordinately into the area of weakened gametophytic tissue at the base of the archegonium by displacing the basal jacket cells. They retain the same apical disparity in size initiated during wall formation in pro-stage. All the apical cells divide transversely soon after rupture of the archegonial jacket. These developments are illustrated by Figs. 12, 13, and 19. In Fig. 19 the two tiers of tip cells form a more pointed cluster than is commonly found. The apical walls are thicker than those of the segments behind. This is similar to the thickening Buchholz (1920a, p. 133) has reported for *Pseudotsuga*. As in *Pseudotsuga* the apical walls lose this characteristic in later stages, but it is sometimes quite persistent (see Figs. 14, 15, 16, 18, and 22). It was also noted on meta-stage embryos of *Larix laricina*, as shown in Figs. 23 and 24. From later developments it now seems clear that this thickened apical wall does not serve effectively to hold the tips together very long past mid meta-stage, although it may be a factor in preventing early cleavage of the separate polarity units such as takes place in pine.

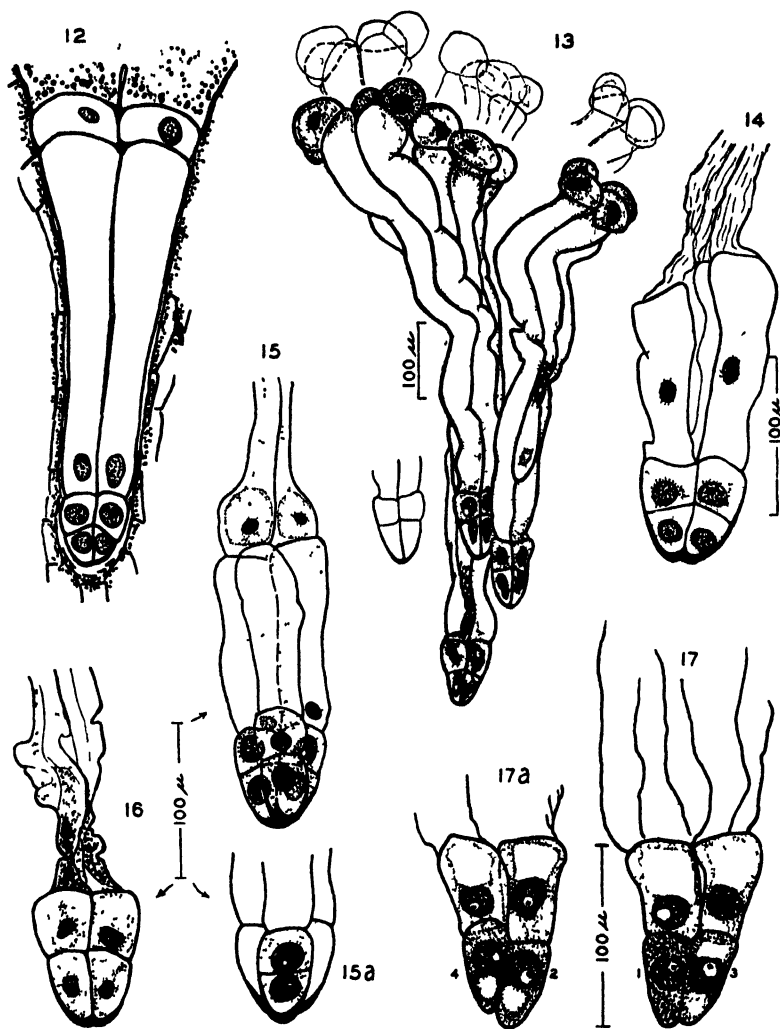


Fig 12—Longitudinal section of embryo system: early meta-stage. Free-hand drawing based on serial sections. Collection of May 26, 1933.

Fig. 13.—Group of three complete embryo systems in early meta-stage, dissected from one gametophyte; details of arrangement of each group of rosette cells is indicated above. Collection of May 28, 1932.

Fig. 14.—Tip of embryo system at time of elongation of second embryonal tubes.

Fig. 15.—Tip of embryo system similar to that of Fig. 14. Fig 15a shows the fourth polarity unit drawn from a lower plane of focus.

Fig. 16.—Tip of embryo system in which the apical cells are more than usually elongated, perhaps preparatory to division.

Fig. 17.—Tip of embryo system, from the same collection as preceding figures but slightly more advanced. Fig 17a is drawn from a lower plane of focus.

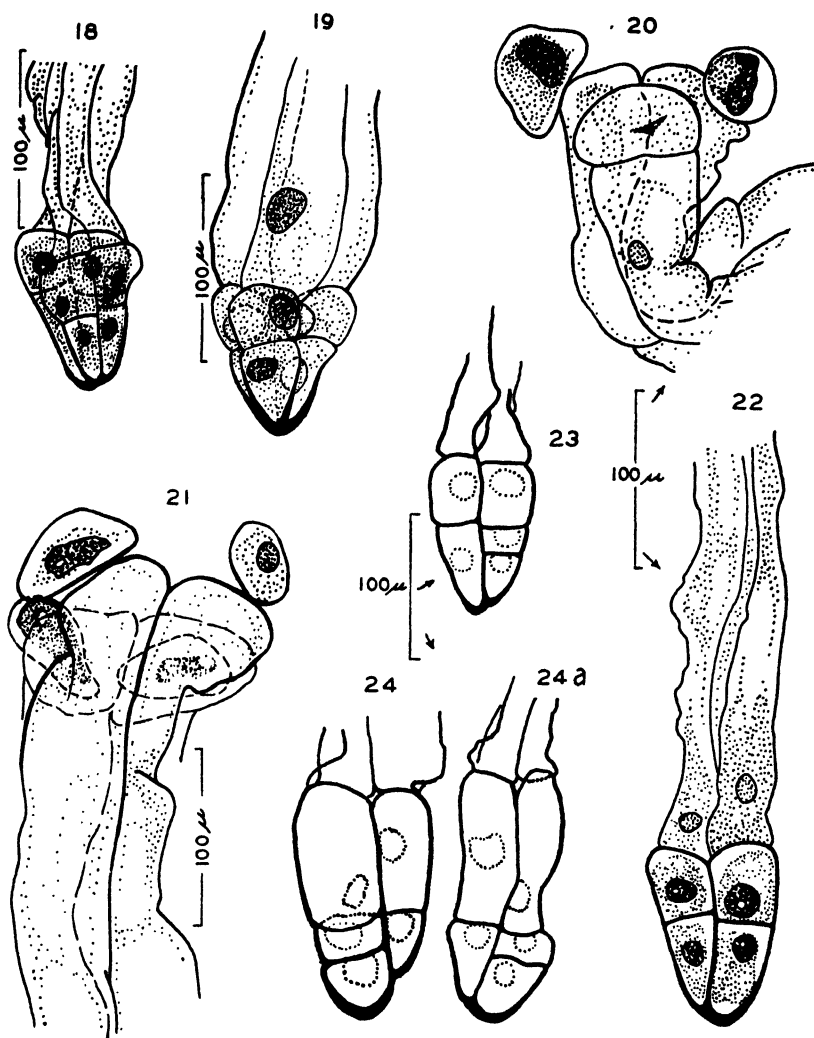


Fig. 18.—Tip of embryo system in which two polarity units on the side uppermost in the preparation are somewhat less developed than in Fig. 17.

FIG. 19.—Tip of very early meta-stage embryo system. Collection of May 28, 1932.

FIG. 20.—Rosette cells and primary suspensors belonging with the tip shown in Fig. 18. Same collection as Fig. 19.

FIG. 21.—Rosette cells and primary suspensor belonging with the tip shown in Fig. 22.

FIG. 22.—Two of the four polarity units of an embryo system showing typical asymmetry.

FIGS. 23 and 24.—Tips of polarity units of meta-stage embryo system in *Larix laricina*. Fig. 24a is drawn from a lower plane of focus. Collection of June 17, 1935, Grass Lake, Michigan.

The tiers at the tip of the embryo system grow in length and the primary suspensor elongates, as shown in Figs. 11 and 12, to move the tip cells deeper into the nutritive tissue. The apical cells divide to form another suspensor segment later on when the primary suspensor cell is collapsing and the first embryonal tubes are elongating. This serves to keep the tip cells pressed firmly against the archegonial tissue, and they slowly progress down the center of the gametophyte, apparently digesting their way. The pressure alone, developed by elongation of suspensor cells, is inadequate to cause penetration of the gametophyte, since these cells collapse readily and lack any strengthening features. The mechanical ability of the suspensor cells is dependent chiefly on turgor pressure developed from within.

The cavity in the gametophyte digested by enzymatic action has been called the corrosion cavity by Buchholz (1918, p. 195). The cavity in *Larix* is lined with a layer of partly digested debris consisting of remnants of gametophytic cell walls and refractory granules, a sort of "pseudo-epithelium." The corrosion cavity undoubtedly contains more or less fluid substance surrounding the embryo and serves as a means of food transfer in solution. Sections sometimes show the embryo tip of *Larix* embryos some distance away from the lower end of the cavity, but others show it in contact at this point. Probably digestive processes precede the embryo tip to some extent, but it is supposed that more efficient and rapid penetration occurs when the tip cells are close to the gametophyte cells acted upon.

For a considerable period of time, growth of the embryo is slow. Basal segments of all four polarity units are cut off successively and elongate in turn to maintain the suspensor. In the course of these processes the thickened apical wall disappears. Cell division is infrequent, and the most obvious result of early meta-stage growth is digestive penetration of the gametophyte by the embryonic tip. For the most part cell division merely keeps pace with depletion due to collapse of previously formed suspensor cells. The tip for a considerable time consists of the apical cells, one tier of more or less unelongated suspensor cells, and then the elongated embryonal tubes (cf. Figs. 14 and 15).

The shape of the rosette cells changes from their original flat form in pro-stage by becoming rounded as shown in Fig. 13. They are from the first much larger than the apical cells of the vertical rows. Later when the primary suspensor is disintegrating they also lose the staining character associated with living cells. Their nuclei become indefinite in shape and the cytoplasm vacuous. In dissected embryos beyond the early stage of elongation they are apt to become dissociated from the primary suspensor cells. Figs. 20 and 21 show rosette cells at this stage, and a little later they disintegrate along with the primary suspensor and are

seen no more. They very obviously lack the meristemátic qualities which distinguish them in *Pinus*.

In later meta-stage the asymmetric arrangement (which characterizes the apical arrangement from the time of wall formation in the proembryo) becomes more obvious. As a result of the tetragonal arrangement in pro-stage, the two larger polarity units gradually increase their superiority. Often one of these two appears superior to the other. This is the case in the tip shown in Figs. 17 and 17a. The four tips lie with two in a high plane and two in a lower plane and have been drawn separately. The order of superiority is indicated by the numbers one to four. The apical cell of the first polarity unit may safely be designated as the dominant one of the group. Not only does this apical cell project slightly ahead of the others but it alone is nonvacuolate. The second unit, on the opposite corner in lower focus, is nearly as advanced as the first, but has a small vacuole above the apical cell nucleus. The third and fourth units are clearly subordinate and must have occupied the narrower angles of the archegonial ellipse in the proembryo. Figs. 24 and 24a show the same arrangement in a meta-stage embryo of *Larix laricina*, but in this case the tetragonal disparity is greater. Fig. 18 shows a different cell arrangement in which both of the minor rows are on one side. In this case one of the polarity units in the lower plane of focus would have become dominant. This arrangement is not frequently found and very likely came from an abnormal arrangement of the proembryo nuclei. The rows shown in Figs. 15 and 15a are not so decidedly asymmetric. Still I have no doubt that eventually only one polarity unit could go on to form the final embryo. The underlying row, shown in Fig. 15a, projects slightly in advance of the others. The tip, illustrated in Fig. 22 (only two units of which are shown), is typically tetragonal in its configuration. Figs. 14 and 16 illustrate the close pairing of opposite polarity units. In both cases the other two units, one located in a high plane of focus and the other below and not shown in the drawings, were noticeably shorter. Figs. 14, 15, and 16 also indicate how rapidly and completely collapse of the suspensor may take place. It is not possible to count how many embryonal tubes have been formed, but in each of these cases probably three or four collapsed segments have been produced for each unit prior to development of those now elongating. The four units composing each system of the three shown associated in Fig. 13 show evidence of tetragonal arrangement when examined individually at higher magnification, although this may easily be passed over in casual observation.

Embryo tips in cross section at this stage also show the same tetragonal configuration. In Fig. 25 serial sections of the tips of two systems are shown, both of which include eight cells above the much elongated cells of the suspensor. The cell nuclei are shown in the section

in which they are most prominent. The system which has grown farthest within the gametophyte extends from section *a* to *h*. Disintegration of the suspensor of this system is quite advanced in the sections beyond this where the tip of the lower embryo system was in contact with it. The apical cells of the lower system are cut in sections *g*, *h*, and *i*. In both of these embryo systems those two units which adjoin each other in the center by a straight segment of wall are seen to be somewhat larger than the two rows which have a single central angle. This is shown particularly by sections *a*, *b*, and *c*, and by sections *g* and *h*, which transect the apices in both cases. The same condition is observed in Fig. 26, which also represents the second embryo system in its particular corrosion cavity. Section *f* of Fig. 26 shows the cavity as enlarged by passage of the two systems; the almost completely disintegrated suspensor of the first system is collapsed alongside the second tip.

Up to this stage each polarity unit has functioned in close contact with others of the group of four derived from a single embryo system. The tips of the various systems have digested their way through half or three-quarters of the length of the gametophyte, the first system to elongate being most advanced. Soon the tendency toward formation of massive

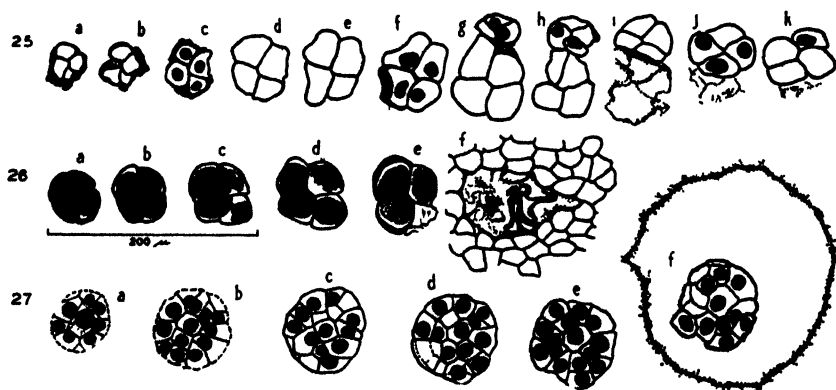


Fig. 25, *a-k*.—Serial cross sections of tips of two meta-stage embryo systems within the same gametophyte. Note that the cells which adjoin by the straight central wall are larger and that suspensor cells of the first system are disintegrated at level of contact with the second system (*h-k*). Collection of May 30, 1933.

Fig. 26, *a-f*.—Serial cross sections similar to those in Fig. 25. The corrosion cavity is shown in *f*, at a level where the suspensors have collapsed; note also the disintegrated suspensor of an embryo system which preceded the one shown.

Fig. 27, *a-f*.—Serial cross sections of early ana-stage embryo. Only a single polarity unit can be identified. The corrosion cavity (outline in *f*) has also been enlarged by another more advanced embryo which is located deeper in the end of the cavity. This series probably arose from an embryo system arrangement similar to that shown in Fig. 26. Collection of June 11, 1933.

tissue appears; first in the system deepest within the gametophyte, and then in the others.

Hitherto each apical cell has cut off new cells (which were added to the suspensor in turn) by straight transverse partition walls. That is, although these apical cells are somewhat triangular in cross section due to mutual contact, they each have a single basal cutting face and are altogether comparable to the hemispheric apical cells of pine at this early stage. The only difference is that the polarity units in pine have separated from each other by early cleavage and are not ordinarily in contact. Buchholz (1918, p. 202) found that in pine the "stage in which the apical cell has two cutting faces does not exist or is so shortened that it cannot be easily recognized." In *Larix* the polarity units ordinarily form several segments from an apical cell with two cutting faces; this is explainable as due to contact between the apical cells of polarity units of the system. Fig. 28 (p. 37) shows two units having apical cells with two cutting faces, one of which has divided cells in alternate planes for the last seven or eight divisions. This is the unit which would have finally become dominant. The two repressed units show less advanced conditions. The one at the left is slightly separated from the rest of the group, and has a nearly hemispheric apical cell; the opposite unit (drawn separately at *a*) is slightly more advanced, having recently cut off two oblique segments.

Fig. 29 shows a somewhat similar stage obtained from sectioned material in which one of the polarity units has become further dissociated, so that it represents a case of normal cleavage. This unit is shown in section *a*. It has been considerably distorted and the apical cell is broader than usual, perhaps due to the unusual circumstances resulting in its cleavage from the rest of the system. The next three serial sections contained no significant embryo parts and are not represented by drawings. The remaining group of three embryo units of this system are shown in successive sections represented by sections *b*, *c*, and *d*. Section *b* shows an apical cell with two cutting faces. The small unit at the right in section *c* has an apical cell with a seeming flat base which has nevertheless produced two wedge-shaped segments. The configuration of segments shown in section *d* shows that the other polarity unit has an apical cell with two cutting faces (most of which is included in section *c*) that has persisted for at least seven divisions.

During the period in which the apical cell has two cutting faces (the stage II apical cell), one polarity unit finally develops to overtop its competitors. When pressure is sufficiently relieved by overtopping the other units, the leading apical cell graduates to a tetrahedral shape and produces segments on three cutting faces. Not only does this occurrence afford the dominant unit the opportunity of forming a massive meristem but it very quickly eliminates the competing units. Only in cases where

Fig. 28.—Tip of late meta-stage embryo system in which two of the polarity units have a stage II apical initial (two cutting faces) and the others only hemispheric initials. Polarity unit *a*, almost hidden in the original group and drawn separately at the right, has segmented obliquely during the last division and presumably is somewhat more advanced than the unit at the left of the group. Collection of June 11, 1933.

Fig. 29.—Tip of late meta-stage embryo system from sectioned material. Sections *b*, *c*, and *d* are consecutive and show three polarity units closely associated. The fourth, represented in section *a*, was separated from the rest and was developing independently; presumably this is a case of ordinary cleavage. Collection of June 13, 1932.

Fig. 30.—Early ana-stage embryo tip which includes the progeny of only one polarity unit. Its section in Fig 30*a* shows no remnant of an apical initial. Collection of June 14, 1932.

Fig. 31.—Early ana-stage tip from the same collection as the last, but slightly more advanced. Derivation rows occur in the mantle layer, as shown in the drawing of the surface; a stunted repressed unit still adheres to the side of the larger embryo. Figs. 31*a* and 31*b* represent sections of the same embryo at successive focal planes.

Figs. 32 and 32*a*.—Surface and section of an embryo tip from same collection as Fig. 31 but showing slightly different proportions.

Fig. 33.—Early ana-stage embryo in which the pleromic centrum and columnar tissue are becoming evident. Collection of June 6, 1933.

Fig. 34.—Early ana-stage embryo, earlier than Fig. 33, showing manner of elimination of the apical cell. Magnification same as for Fig 36. Collection of June 13, 1932.

Figs. 35 and 36.—Sections of early ana-stage embryo tips, showing wedge-shaped mantellary cells which are tentatively identified as remnants of apical cells of polarity units. Collection of June 4, 1933.

Fig. 37.—A pair of early ana-stage embryo tips, with suspensors intimately connected, probably derived by cleavage from the two stronger polarity units of one embryo system. The embryo to the right has eliminated its apical initial, but the tetrahedral (stage III) initial still persists in the other. Collection of June 14, 1932.

Fig. 38.—Tips of two polarity units in more than ordinarily intimate association. Apical initials of both have been eliminated. Non-vacuolate cells are stippled. Both these polarity units would have been repressed by progeny of a more advanced embryo ahead of them in the corrosion cavity. Collection of June 18, 1932.

Fig. 39.—Section of ana-stage embryo showing pleromic centrum and columnar tissue. Collection of June 11, 1933.

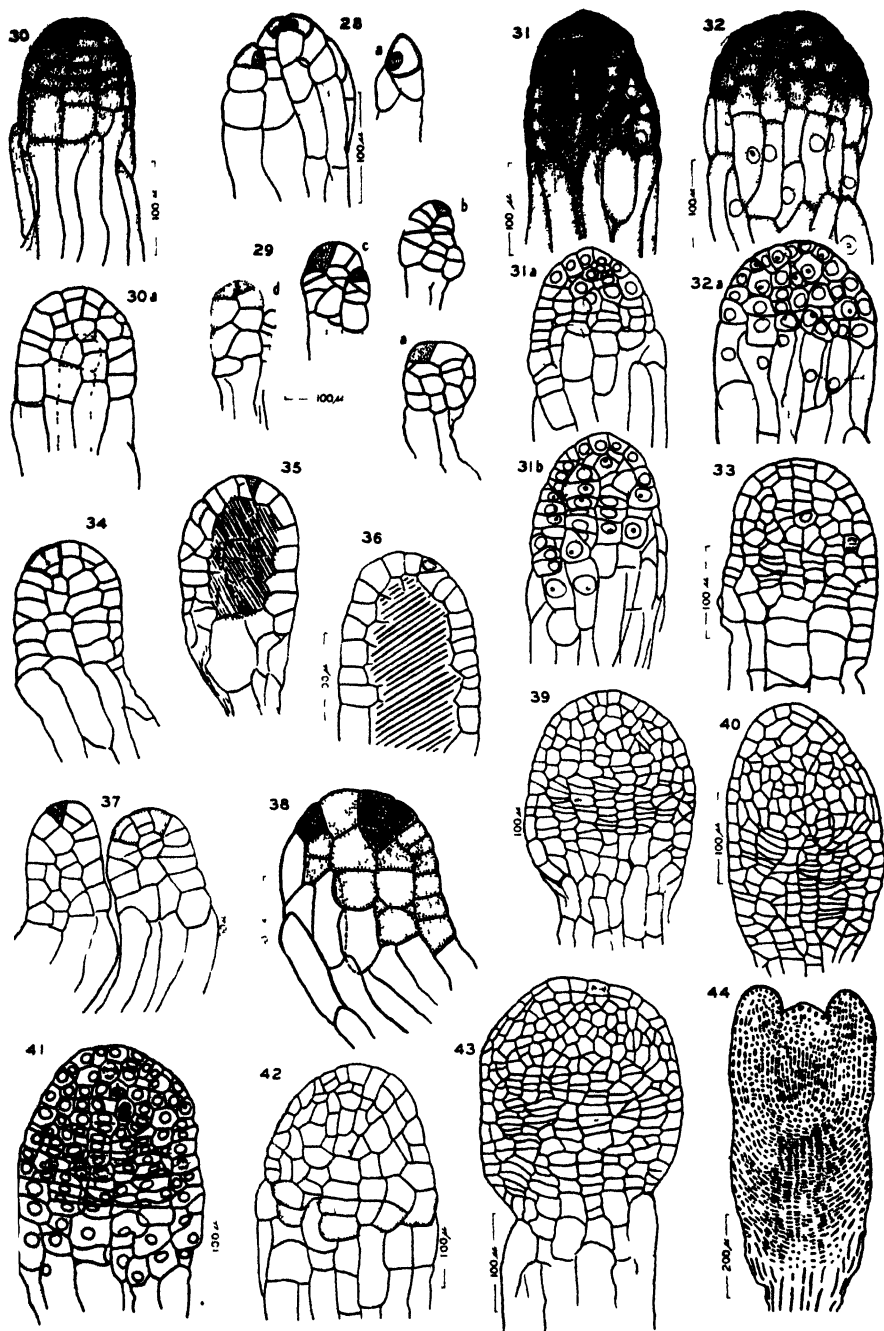
Fig. 40.—Section of ana-stage embryo probably more advanced than that in Fig. 39. The basal curve of the pleromic centrum is better defined, and there is definite tilting of the marginal derivation rows. Collection of June 11, 1933.

Fig. 41.—Section of ana-stage embryo comparable to Fig. 39, with mitotic figures indicated, suggesting the rapidity of growth. Collection of June 6, 1933.

Fig. 42.—Early ana-stage embryo, with stippled line indicating limit of non-vacuolate cells. Collection of June 14, 1932.

Fig. 43.—Section of typical mid-ana-stage embryo, with pleromic centrum clearly defined. Collection of June 11, 1933.

Fig. 44.—Cell line diagram of early telo-stage embryo for comparison. Each line represents the long axis of a cell. Collection of June 25, 1932.



Figs. 28-44.—See explanations on opposite page.

a smaller unit has become sufficiently dissociated from the rest of the embryo system by actual cleavage, and is thus permitted a more independent development, can lesser units survive for any time at all. In such instances they develop their own tetrahedral apical cell and may continue for some time. This appears to be unusual, however, and the isolated unit in section *a* of Fig. 29 is one of the few cases in which characteristic cleavage can be demonstrated. The most usual course seems to involve rapid and complete subordination of the smaller polarity units.

The dominant embryo unit by this time has a tetrahedral (stage III) apical cell which is actively building a massive primordium. Occasionally a repressed unit may be demonstrated in connection with the massive embryo primordium, as in Fig. 31c, in Fig. 38, or (with less assurity) in Fig. 35. Fig. 56 (Plate I) shows a later embryo with a repressed unit, with its stage II apical cell still associated. This is unusual since most of the smaller embryos are badly disintegrated before this stage. Generally the fate of the repressed units is quickly sealed when one member attains sufficient dominance to form an apical cell with three cutting faces. Of course, from this stage on the quadrate cross sectional form of the early embryonal system (due to association of the four polarity units) is no longer present.

It is likely that cleavage also occurs in a small percentage of embryo systems where two opposite polarity units are large and strong and evenly paired. Such a condition is probably represented by the embryos shown in Fig. 37. These two embryos, closely associated and nearly the same size, attached together by their secondary suspensors, probably represent the co-dominant units from one originally "tetragonal" embryo system. Absolute proof of this would require tracing the tips of the two units back to their respective primary suspensor cells. However, the primary suspensors, and several embryonal tubes as well, have been so disintegrated that they are not to be found. Embryos of this size generally lack primary suspensor cells since these cells apparently disintegrate within the corrosion cavity soon after their collapse. Evidence that these two are from one, and not two, archegonial systems is derived from the nearly equal size of the two tips and from the condition of the secondary suspensors of both. We have seen (Figs. 25 and 26) that a second system growing along the path of an earlier system rather completely digests the suspensor of the latter as it grows along. Since the suspensors behind the two tips in Fig. 37 seem to merge and to be equally collapsed on both sides, they have undergone similar disintegrative processes such as would not be likely to occur if two separate systems were involved.

Organization at the apices of these two closely matched embryos is the greatest point of contrast. The embryo on the left has a definite well marked apical cell cutting off segments in three planes, while the one at

the right is more advanced and has eliminated its apical cell. This one would probably have become dominant, and it is likely that it held a slightly more advanced position within the gametophyte than it now shows in the dissected preparation. These presumably twin embryos show how soon the single apical cell may be eliminated. Both contain about 60 nonvacuolate cells (as computed according to the formula given by Buchholz 1918, p. 213). There is nothing to suggest that these embryos are abnormal in development, although they probably have come from a system with cleavage more pronounced than usual.

A few other cases have been observed in sectioned material where two embryos of comparable mass were developing within the corrosion cavity which might have come about by similar cleavage. Some persist during stages of later development such as shown in Fig. 47a. No actual proof of derivation can be advanced at such a stage because all the early suspensor is indefinable and even the original number of archegonia is doubtful. From the order of events in pro- and meta-stage, derivation from a single well-balanced embryo system would seem quite possible, however. If a similar situation were found which had developed from a single archegonium, a rare occurrence in *Larix*, this would constitute direct evidence of cleavage. It is likely that cleavage of this type does occur occasionally in *Larix*, although it must be regarded as exceptional, because most of the embryo units remain in contact with the other three units of the system until one becomes overwhelmingly dominant.

Late meta-stage embryos of *Larix laricina*, *L. kaempferi*, and the hybrid resulting from *L. decidua*  $\times$  *L. leptolepis* or its reciprocal (sometimes called *L. "eurolepis"*) have been examined in this stage, and all these conform closely to the description just presented for *L. decidua*. In *L. laricina* the disparity between the four polarity units seems to be a little greater than in *L. decidua*; the others seem to be practically the same.

Whether we call the competitive elimination of repressed units *cleavage* or not, it is clear that the process is similar to that found in pine, differing only in degree. Clearly, it is not correct to assume that the four polarity units developed by the proembryo all contribute to the final embryo even though they do generally remain united throughout meta-stage. Thus simple polyembryony is a misnomer as applied to *Larix*; it has the general embryogenic sequence, with its embryonal competition, etc., essentially as in pine, where cleavage is most characteristic. Obvious competition in *Larix* is merely postponed for a time and then becomes very acute during the phase of actual embryonic selection. From the illustrations given by Strasburger (1872, Pl. XII, figs. 35 to 37, esp. 37) of *Picea* embryo systems in late meta-stage, it seems probable that the same developments occur in this genus. Pseudotsuga and other pinaceous genera previously thought to possess simple polyembryony also may very

likely be similar to *Larix* in this respect. Hutchinson's (1924) figures of *Abies* embryos, as discussed later (p. 65), indicate that the same sequence probably occurs in that genus.

In order to clarify the situation in regard to *Larix* and others like it, it is suggested that the condition wherein the polarity units remain closely associated until late meta-stage, when a dominant one is selected solely to contribute to the final embryo in a manner essentially similar to that found in *Pinus*, be known as *delayed cleavage polyembryony*. In this way the qualitative similarity to *Pinus* is rendered apparent by the terminology. Among gymnosperms simple polyembryony in a primitive sense is best typified by Cycads. True simple polyembryony is more likely an advanced character wherever it occurs in the Coniferales.

#### THE LATE EMBRYO

*Ana-stage*.—When a polarity unit becomes equipped with an apical cell having three cutting faces (the stage III apical cell), growth of massive embryonic tissue proceeds very rapidly. The stage III apical cell usually exists for a very short time, but with respect to number of divisions, it cuts off more segments than either the stage I or II apical cells which preceded it, because the rate of growth increases enormously at about this time. The embryo tip at the right in Fig. 37 shows an early stage lacking an apical cell. Fig. 55 (Plate I) shows the latest stage found possessing an apical cell, but here the last tetrahedral vestige is not dominating growth by any means, and is more properly considered an adjunct to the outermost cell layer or mantle. The manner in which the apical cell is eliminated is suggested in Figs. 35 and 36 where anticlinal division has left a triangular relict of the apical cell inserted in the mantle layer, and in Figs. 34 and 38 where the main apical cell has been segmented by a periclinal division, leaving the triangular segment within the mantle layer.\* This method seems to be quite common, leaving a cell in the central region resembling an "internal" apical cell. Whether the apical cell is finally eliminated by a periclinal or by an anticlinal division seems to be the determining factor; this is probably a detail of little consequence, for before its actual disappearance the essential physiological attributes of the apical initial seem to have been transferred to a deeper seated group of cells.

A normal-appearing tip is shown in Figs. 30 and 30a in surface view and optical section respectively after the apical cell has been eliminated. The characteristic evenly rounded surface over the hemispheric non-vacuolate tip is apparently due to the organization of the external layer of cells designated here as the *mantle* (see footnote, p. 22). This layer

\*The number of non-vacuolate cells in Fig. 34 is about 80, obtained by applying the formula  $lwr^2$ .

is shown in Figs. 35 and 36 and in other embryos of later ana-stage. It differs but little histologically from the cells within, dividing periclinally on occasion, as well as anticlinally. The layer probably constitutes the absorbing organ of the embryo and may be the enzyme-excreting organ (even though enzymes may be first formed in deeper cells). The fact that it acts effectively to preserve the symmetrical, even external contour of the embryo through most of its subsequent development makes it interesting from a physiological and, in the absence of experimentation, from a speculative point of view. Priestley (1928, p. 11) has given some consideration to the contour of more mature plant meristems compressed between "the limiting cuticle and external cellulose wall on one side—and the vacuolated cells on the other," but the ana-stage embryo has no cuticle. For the present the problem of how the mantle effectively maintains a smooth surface contour remains unexplained. We may say that it is due to forces of inherent polarity in the young organism, but this is hardly an explanation of the phenomenon. Once the mantle is uniformly established it probably insures against further subdivision by cleavage or other sort of fragmentation.

After elimination of the apical cell the massive tip often approximates a hemispherical form and for a time grows about equally in breadth and depth. The original segmentation of the apical cell is soon obliterated by repeated cell divisions lacking any segmental regularity. Study of transverse sections of embryos at this stage, such as those shown in Fig. 27a-f, show conclusively that no histogenic demarkation occurs until later. In Fig. 27a the large central cell (in the mantle layer) may be an immediate descendant of the original apical initial, but there is no indication that it or any other *individual* centrally located cell of the embryo possesses special attributes. In this instance cells about 95  $\mu$  below the tip (Fig. 27f) are becoming vacuolate and contributing to the suspensor. Figs. 32 and 42 show tips of comparable but slightly larger embryos in surface view and longitudinal optical section.

The first evidence of histogenic development of the tip is noted in the meristematic cells just above the suspensor. Cells of this region divide more often in the transverse plane and give rise to what I have called columnar tissue. A substantial group of morphologically unoriented tip cells remains above them and functions as a single generative meristem, which as a whole appears to have the polarity attributes formerly vested in the single apical initial. Cells basal to the generative group divide with greater frequency than those above and practically always, it seems, in a plane transverse to the axis of polarity. Consequently, in assuming the columnar habit of growth, each cell gives rise to a filament composed of short flattened segments. Through mid ana-stage, at least, the individual derivation of these filaments is especially evident. Later and in telo-stage

some segments of these filaments themselves generate filaments having a rather marked individuality. The filaments or rows of cells arising from a single cell by repeated division in the same plane may be designated as derivation rows. The columnar tissue which originates in early to mid ana-stage (see embryologic sequence chart, p. 18) is composed of the derivation rows.

The mantle layer also partakes in this mode of growth at this period, just as the centrally located cells, and the tips of these surficial derivation rows may even be identified nearer the apex than those located internally. Fig. 31 shows mantellary derivation rows as they appear in surface view, and this should be contrasted with Fig. 32. Figs. 31a and 31b are optical sections showing the early development of internal derivation rows. The generative group at the tip of this embryo is somewhat smaller than usual, and consequently columnar growth is more evident. The processes exemplified are, however, entirely typical. The inception of columnar growth is seen in surface and optical section views in Figs. 30 and 30a. Fig. 33 is drawn from a section and shows a more rounded terminal outline and larger group of generative cells than Figs. 31a and 31b (with which it should be compared), although both are at about the same stage of development. Fig. 41, also from sectioned material, shows a slightly more advanced stage with a large number of cells in process of division. In the generative region division is in several planes; cell division in the columnar zone in early and mid ana-stage seems nearly, if not entirely, restricted to a plane exactly transverse to the embryo axis.

Increase in embryo length is not proportionate to the number of cell divisions, since only a relatively small number of cells elongate, i.e., only the most basal derivation row segments. Other row segments actually diminish in average size by the numerous transverse divisions. The suspensor cells derived from columnar tissue do not grow to the great length characteristic of the earlier embryonal tubes, but only go to one-half or a third the length before collapsing. Nevertheless due to the greater number of cells contributing, the suspensor increases in prominence during this stage, becoming not only much longer but broader, as the tip increases in width.

The "unoriented" group of generative cells above the derivation row initials also increase greatly in number. After it becomes rather definite this region may be designated as the *pleromic centrum*, since the plerome is derived from it in later growth. The lower border zone of the pleromic centrum is necessarily indefinite. The section illustrated in Fig. 39 shows a narrow layer of columnar tissue below the pleromic centrum—at this time an undifferentiated meristem somewhat hemispheric in form. In Fig. 43 (also from a section) the shape is much the same, but broader, with a deeper zone of columnar tissue below. Similar stages are shown

in Figs. 55 and 56. An entire embryo tip is shown in Fig. 62. The diameter of this embryo is about  $250\ \mu$  at the base of the centrum. Fig. 58 shows an embryo tip of similar diameter at somewhat greater magnification, but with a considerably greater depth of columnar tissue below. The length of the whole non-vacuolate meristematic tip is about  $455\ \mu$ .

The base of the pleromic centrum in all these instances is flattened with a slight convex curve. As the embryo becomes older the basal convexity becomes more marked. The sectioned embryo shown in Fig. 40 shows this advance with reference to the basal curve of the centrum and is in a more advanced stage of development than that in Fig. 43, even though it is somewhat smaller. The arcuate contour and its effect on underlying derivation rows is readily noted. The central derivation rows are oriented normally along the central axis of the embryo, but those formed on either side are tilted to conform to the basal curvature of the pleromic centrum. The effects of this are made clear in study of embryos beyond the stage of development shown in Fig. 58.

In the mature embryo the calyptroperiblem is composed of two embryonic tissues. The column (*periblemsäule* of Schacht) consisting of what has been described as columnar tissue extends straight down from the tip of the plerome to the massive suspensor. The second tissue arises from the column and lateral to it following mid ana-stage. This lateral tissue is called *peri-column* since it is immediately derived from the columnar tissue and surrounds it on all sides. The origin of the *peri-column* from the marginal tilted rows extending from the base of the pleromic centrum down around the sides of the columnar tissue and the consequent diametric enlargement of the embryo is described in some detail below.

The normal plane of cell divisions in columnar tissue is, as previously stated, transverse to the organic axis and to the axial polarity of the organism. When the more marginal derivation rows become sufficiently tilted so that they are no longer even approximately parallel to the axial polarity, they tend to deviate notably from the ordinary course of cell division typical of a simple derivation row. Instead of customary vertical multiplication, lateral elongation and division takes place among the component cells of the tilted rows. Axial polarity is effective in governing divisions within the derivation rows so long as the latter are approximately parallel to it. At a certain angle of tilting the cells become freed from their subordinate status within the row, and each one then becomes competent to divide in accord with the plane which would ordinarily be associated with its flattened shape.

Sachs's law, as given by Priestley (1928, p. 10), that "*when a protoplasmic mass divides into two, the two daughter cells will be equal in mass,*" is fairly approximated throughout the course of growth in all

these embryo tissues. In the columnar tissue, however, Errera's law, as stated by Priestley (*loc. cit.*), "*that when a cell division takes place the semi-liquid dividing wall tends to be of minimum area, if the dividing cell is in equilibrium with its external surroundings,*" serves to emphasize that the derivation row segments (in normal alignment) are not *individually* in equilibrium, although the row as a whole, if considered as a sort of supercellular unit, may be relatively well equilibrated. The normal division of all cells in the columnar tissue derivation row is across the *broadest* area of the cell; but when tilted, as shown by marginal rows in Fig. 40 for example, an individual equilibrium is newly attained in each cell to make it essentially independent from its previous row affiliation.

At such a time the cells divide at right angles to their former plane of division, forming a wall across their short dimensions in a direction which is quite definite. This first wall is placed radially from the embryo axis. As a result each originally round flattened coin-shaped row segment now consists of two halves, each cell of which has its long axis directed away from the center of the embryo. The manner of division is best illustrated here in Fig. 85 (Plate VI) in the calyptroperiblem of a telo-stage embryo but is easily demonstrated in other transverse sections after the pericolumn has begun to form. Subsequent to the primary radial division of the tilted columnar cells Errera's law is strictly followed. The next walls produced are of minimum area and at right angles to the first, forming across the short diameter of each cell. Hence these second walls are laid down in a plane obliquely tangential to the embryo axis. This manner of addition to the pericolumn continues typically through the telo-stage and, on a somewhat restricted scale, even in the seedling.

The process of reorientation of polarity goes on all around the columnar tissue in general accord with the generalized radial symmetry of the embryo. Thus essentially the same degree of tilting occurs in all the marginal rows around the girth of the embryo, and the same series of divisions occurs in each of the row segments when they become free of their derivation row linkage and the component cells *individually* attain an equilibrium with the forces of polarity.

Axial cells of the columnar tissue tend to become smaller in their vertical dimension as divisions occur, up to a certain minimum, with only relatively slight equivalent expansion following each transverse division. In the cell line diagram shown in Fig. 44 the greater number of cells thus present within the column is emphasized. But in the individually equilibrated cells around the columnar tissue, equivalent expansion takes place following each mitosis. This expansion must take place in a radial direction because the cells all around the columnar tissue have developed and are exerting pressure on the various sides. The cells therefore are chiefly able to increase only in length.

The continued growth of the peri-column through late ana-stage and in early telo-stage has much to do with the final diameter of the mature embryo. Primary axial polarity does not seem to function directly in producing lateral enlargement beyond a diameter of about 300  $\mu$ . The mature embryo may become nearly twice as broad as this. Peri-columnar growth is not only directed radially but it also has a marked upward trajectory, derived from the tilt of the marginal rows in the columnar tissue. This makes it possible for the lower parts of the column to supply peri-columnar offshoots sufficient for nearly the whole of the calyptroperiblem. The primary origin of the periblem itself is to be found close to the top of the column, where the marginal derivation rows are shortest and most extremely tilted.

Derivation rows close to the zone of row initials at the top of the column are very short and consist of only a few segments, since they have begun columnar growth most recently. Many of these around the margin of the initial zone are tilted at a considerable angle in conformity with the basal curvature of the pleromic centrum. These topmost marginal derivation rows never get very long because their component row cells soon become individually equilibrated and proceed to follow a course of lateral growth in general as outlined above. The potentialities of these topmost lateral offshoots differ somewhat from those lower down, however, due to their position near the sides of the pleromic centrum. Even when the calyptroperiblem is rather well developed the centrum is quite small. In late ana-stage when the centrum begins to develop more rapidly, derivatives of the marginal topmost derivation rows are in position around it. The peri-columnar tissue lower down ceases active growth early in telo-stage when the calyptroperiblem has nearly attained mature embryonic size, but this is not true of the uppermost offshoots of the column. They continue growth in early telo-stage concurrent with the growth of the plerome. The upward angle of growth, already extreme, becomes more pronounced in their cellular progeny. The direction of growth alters in a gradual curve until it is parallel with the axial polarity and with the plerome. Thus the periblem *originates in a manner similar to the peri-column*. Later growth of periblem and plerome is essentially intercalary in nature, normal axially aligned rows of cells being formed from the various initials in place there. The lateral component of growth from columnar tissue is in great part directly responsible for the increase in diameter of the late ana-stage embryo over the early ana-stage. Massive multiplication of cells, such as constitute the pleromic centrum, is responsible for very little of the increase in embryo diameter in late ana-stage and telo-stage development. Even in the telo-stage embryo the rows of periblem cells are still clearly traceable back to their primary source on the upper margin of the peri-column.

The columnar tissue may be regarded as a source of meristematic tissue for lateral enlargement throughout middle and late ana-stage and early telo-stage. Peri-columnar growth starts from the top of the columnar tissue and works down rather rapidly. Marginal columnar cells that remain, next undergo essentially the same process of growth laterally. The process may be likened to a systematic sapping of the columnar tissue. As mentioned before, derivation row segments of the column tend to diminish in size due to lack of equivalent expansion after mitosis. The lateral offshoots of the column, which make up the peri-column, regain this capacity for equivalent enlargement of daughter cells. The basal cells of the column (and also of the peri-column to some extent) continue to contribute to the massive suspensor. The suspensor cells are the only ones in the embryo to lose their meristematic character and undergo maturation enlargement and vacuolation, but from the standpoint of the columnar tissue, lateral depletion is most important and it tends to decrease the transverse dimension of the column proper throughout late ana-stage. Basal contribution to the suspensor takes relatively few cells, and this is more than compensated by the extremely active transverse division of cells in the derivation rows. Consequently the column grows considerably in length during middle ana-stage to early telo-stage.

The longitudinal growth of the column is important in explaining the tissue configuration of the calyptroperiblem, which is the first part of the full grown embryo to attain embryonic maturity. So long as columnar derivation rows remain near the center of the tissue, growth remains essentially unchanged. Very occasionally a vertical wall may be produced near the middle of an old derivation row and a new series of row cells started from each of them, but this seems to be of little significance. In general the central derivation rows near the base of the column are relatively longer than those nearer the top of the column which originated later. The cells of these oldest columnar rows are also somewhat broader than those above. Marginal rows in the basal portion have been contributing to the peri-column somewhat longer than those above and consequently, at the base of the column in middle and late telo-stage embryos the typical derivation row groupings are larger but fewer.

The first cells to produce offshoot lateral tissue in the calyptroperiblem dominate the appearance of the lateral tissue because they redivide and likewise form a type of derivation row. The constituent cells of these rows are very different from those of the column in that they are elongated and join end to end. They are not so obviously derivatives of single cells, yet on closer study it is clear that their sequential derivation in series is almost as marked as it is in rows pertaining to the column itself. Certainly the planes of cell division are very definite and just as

characteristic as before. The cell division plane in peri-columnar tissue is essentially at right angles to the plane of characteristic cell division in the column. For reasons explained below actually the plane of peri-columnar cell division is somewhat more than 45 degrees removed from the columnar cell division plane, but the first division is at about that angle. Deviations in excess of that angle occur increasingly, so that the files of cells appear to be bent in an arc, and, in the case of rows of cells entering the periblem, the plane of division actually has been *totally reversed*, so that it again coincides with the original transverse plane of columnar division.

Elongation of the column occurs concurrently with growth of the peri-column and, consequently, this produces interstitial tension among peri-columnar rows. One way this tension is relieved without formation of large intracellular spaces is by the offshoot rows reclining more steeply in an upward direction. Another factor which also relieves this tension is addition of shorter interstitial offshoot rows from marginal columnar rows which were at first entirely within the column. All cells of the embryo (except the suspensor cells) are meristematic and plastic and they readily accommodate themselves in spacial relations. The point to be made is that a very definite rearrangement is necessary. In telo-stage the oldest and longest lateral derivation rows are very considerably curved in the basal region of the calyptroperiblem. Longitudinal growth of the column is one responsible factor; another factor (in which cause and effect are hard to distinguish) involves the shorter lateral derivation rows which are introduced between the longer files of cells. The photo tracing reproduced in Fig. 45 illustrates this condition in an embryo at telo-stage.

A rather sharp break generally is seen at the surface of an older embryo, where lower lateral derivation rows limited to the calyptroperiblem lie against rows which continue up into the periblem of the axis. This line encircling the embryo may be called the *juncture zone*. It is generally a distinct feature in the external contour of the embryo, not only due to the slightly greater diameter of the embryo often found above it, as in *Larix*, but also to alteration of the mantellary layer covering the peri-column below. Beneath the superficial layers there is no morphologic distinction between the rows that continue into the periblem and those which are limited to the peri-column. The juncture zone in *Larix* is consistently at about the same level as the tip of the plerome. It can be distinguished from middle to late ana-stage up to embryonic maturity. It is indicated by the letter "J" in Figs. 57 to 61.

Above the juncture zone the mantle maintains its normal relations, accommodating itself to the underlying growth and occasionally adding to the tissue within by a periclinal division throughout ana-stage and early

telo-stage. Below the juncture zone the mantle cells become distorted in shape and transformed so that they are finally not easily recognizable as being derived from the original external layer. As shown in Fig. 31, some of the mantle cells form derivation rows similar to the cells within. The mantle layer at a later stage, as shown in Figs. 39 and 43, is not partaking in this form of growth, due to the necessity of expanding by both longitudinal as well as transverse anticlinal divisions to cover the

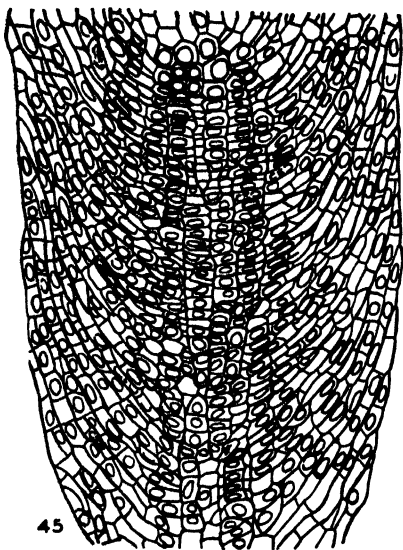


Fig. 45.—Section of calyptroperiblem from mid-telo-stage embryo, showing how mantellary cells have become wedge-shaped because of growth pressures. Magnified 140 times. Collection of June 25, 1932.

considerably greater surface resulting from the increase in size. But with the advent of peri-column, the mantle cells are subjected to oblique tangential pressure from cells within, which distinctly modifies their form. The walls pressing from within abut on parts of the mantle cells and shape them. In addition a "drag" tension is transmitted successively downward from one calyptroperiblem cell to the next. Mantle cells are generally larger than the cells of lateral derivation rows, and hence a single mantle cell frequently terminates more than one lateral cell series. Fig. 60 shows the mantle before it has been irretrievably distorted, but downward from the juncture zone the cells become increasingly oblique in form until near the base they are triangular and tip upward at an acute angle. All calyptroperiblem mantle cells of later telo-stage embryos are distorted in this way, as shown in Fig. 45. Occasionally gaps occur where mantle cells are pushed apart and a marginal cell is seen which is derived directly from the peri-column. However, the majority of surficial cells of the calyptroperiblem, as elsewhere, are derived from the original superficial layer which originated very early in ana-stage.

The juncture zone is chiefly distinguishable due to the distorting pressure which has been exerted on the mantle cells below it. Cells above the zone are not subject to this sort of pressure. In Fig. 60 and in later stages just at the juncture zone one layer of the peri-columnar cells seems almost continuous with the mantle layer above. This arrangement is a derived one, produced from constant internal pressure directed obliquely

upward by this one row (layer) of cells against the continuous mantle of the axis while the embryo diameter was expanding in this region. The continuity of rows inside the axis mantle, with rows in the upper part of the calyptroperiblem is, of course, due to actual continuity in derivation.

Fig. 58 shows an ana-stage embryo in which the peri-column is only starting to be formed. This embryo is slightly more than  $250\ \mu$  wide at the broadest portion and has no definite periblem. The pleromic centrum is nearly spherical, occupying the upper central region within the mantle. The plumule primordium will arise at the tip by multiplication of cells derived both from the upper part of the pleromic centrum and from periclinal division of the mantle. Along the sides, near the juncture zone, the upward sloping mantle cells of the peri-column are beginning to appear, but the juncture zone has not yet become easily distinguishable. Fig. 59 shows a later stage in which a few lateral series of cells have been formed on all sides nearly the length of the calyptroperiblem. A few of the highest calyptroperiblem series have added to the periblem region by intercalary growth, and the plerome has concurrently elongated. The place where the juncture zone is developing may be seen. The plumule primordium has developed its maximum prominence; hereafter the shoulders on either side will build up, eventually to form cotyledons. The embryo now exceeds  $300\ \mu$  in width, chiefly because of formation of tissues lateral to the pleromic centrum. Fig. 57 shows continuation of development seen in Fig. 59. The diameter in the upper part has increased to nearly  $400\ \mu$ , and the next step is development of cotyledons on the shoulder surrounding the plumule primordium.

The formation of cotyledons seems to be initiated with development of a small-celled more meristematic plate of tissue which first serves to divide the plumule primordium from the pleromic centrum. This plate is the cotyledonary "node," and it extends laterally coordinate with the radial enlargement induced by formation of periblem tissue. There is also some contribution to the cotyledons from the mantle. The length of the embryo shown in Fig. 57 (exclusive of the suspensor) is about  $940\ \mu$ , of which the plumule primordium occupies about  $100\ \mu$  and the axial (plerome) region about  $250\ \mu$ . The calyptroperiblem is the longest component and has more nearly completed its embryonic growth than any other part. It may be noted that the shoulder at the right in Fig. 57 is slightly more developed than on the opposite side, a feature indicating cotyledon asymmetry as previously noted by Buchholz (1919, p. 115). Longitudinal sections taken in late telo-stage (Figs. 63, 65, 66) show that cotyledons do not generally develop equal in size.

Primordia of the usual five or six cotyledons appear as separate prominences around the margin of the cotyledonary shoulder growing up

around the plumule primordium and obscuring it from view.\* No lobing of cotyledon primordia, as reported by Buchholz (1919) for other genera, was observed, although probably an insufficient number of embryos was examined at the most favorable stage for observation to support a definite conclusion that this never occurs.

In telo-stage the calyptroperiblem will come to exceed its late ana-stage length by about one-third, while the axis becomes more than twice as long. Fig. 57 shows the late ana-stage condition, and Fig. 61 shows a telo-stage embryo about two-thirds grown. Diameters in the upper portion of the axis in Fig. 61 are not reliable, since this embryo was slightly crushed, but because of this it was more translucent and more easily photographed.

*Telo-stage.*—Ana-stage has been defined as the period in which the embryonic tissues originate, and telo-stage, which follows, is the period of maturation of these tissues leading up to the dormant or resting stage of the embryo. Growth is chiefly confined to progressive enlargement of the several embryonic tissues that were previously initiated. Thus there is no distinct boundary to be drawn separating telo-stage from ana-stage development, but the cotyledonary tissues arise last and so the inception of this last growth period may be recognized by the appearance of localized primordia which are to become the cotyledons.

The cotyledonary primordia develop on the shoulder of tissue around the plumule meristem. Certain smaller cells identified with the nodal primordium are instrumental in forming the cotyledon anlage, and later, the cotyledonary procambia. The trend of these nodal cells extending toward the stubby cotyledons is seen in Fig. 60, and an extension of the nodal primordium downward on the sides of the plerome soon becomes visible. The nodal region is recognized as first in procambial differentiation; the procambia of cotyledons form as they grow, and pleromic procambia form slightly later as downward extensions of differentiation from the nodal region. It is indicative of this same trend that the first tracheids to be seen in germinating seedlings also occur in the nodal region.

In growth of cotyledons a few rows of cells such as those typical of the periblem extend upward outside the incipient procambial strands. A few of these rows on the abaxial sides may be derived from the periblem cells with original derivation from the base of the plerome, but most of them come more directly from the few cells formed at the upper lateral margin of the pleromic centrum. They may be seen adjoined at the ends of the periblem cell series, bearing an analogy to derivation rows of columnar tissue, with the important difference that each cell division is

\*Butts and Buchholz (1940) have presented statistical data on cotyledon numbers in *Larix* and other conifers.

followed by proportional size increase of the daughter cells to maintain a fairly constant average cell-size. They are similar in general character to the derivation rows of the periblem. The dermal layer soon becomes very definite over the cotyledons and essentially ceases periclinal division. The mantle over the upper portion of the axis also graduates to stability in showing only anticlinal division and such features as are generally associated with a dermatogen. It becomes more and more strictly a histogenic layer adapting itself to the increasing mass within by anticlinal segmentation. The external layer of cells over the plumule primordium, however, never seems to become differentiated to this extent.

Secretory elements of a variety infrequently recorded become established in the early telo-stage embryo and persist until sometime after germination. On account of their persistence several who have studied seedlings of conifers have described them, Messeri (1935) being the most recent. She illustrates cross sections of young seedlings of *Pinus halepensis*, *Cedrus libanotica* [sic],\* *Larix europaea*, *Abies cephalonica*, *Pseudotsuga douglasii*, *Tsuga canadensis*, and *Picea orientalis* and finds similar secretory elements in all. She considers the dark-staining contents a feature of the protoplast because she found what appeared to be a thin cytoplasmic membrane surrounding the dense secretion. Chauveaud (1903a) was the first to definitely call attention to these structures in the embryo. Among other conifers he worked with dormant seeds of *Cedrus deodara*. This account of the dormant embryo of *Cedrus*, featuring these secretory elements, has seemingly been overlooked by most subsequent investigators. Hutchinson (1917) briefly discusses their occurrence in the embryo of *Keteleeria* as "mucilage" canals. There can be no doubt that these structures correspond to the secretory elements now described from the *Larix* embryo.

In *Larix*, as in *Cedrus*, and the others of the Pinaceae, the secretory elements are of two varieties, distinguished chiefly by their position—pleromic and subdermal. They are first seen in the central region of the plerome, and early stages of pleromic elements are shown in Fig. 46, *c*, *d*, and *e*. In telo-stage embryos it is customary to find eight or ten of these extending from the region of initials at the base of the plerome up through the axis. In Fig. 46, *c* shows two of them closely associated in the central part of the plerome. Their lower tips are only a few cells removed from the basal pleromic arc (indicated by broken line). In all instances the nuclei are large and elongated, with several dark-staining "nucleoli" within. The cytoplasm is granulose and diffuse and not yet deep-staining. Later on, all the cellular structures become obscured by the dense contents, so that a nucleus could hardly be identified by ordinary staining

\*According to Rehder (1940), the legitimate name is *Cedrus libani* Loudon.

methods if it were present, but Messeri's conclusion as to their essential cellular constitution seems justified.

Subdermal secretory elements at an early stage of development are shown in Fig. 46, *a* and *b*, similar to the pleromic elements in *c*, *d*, and *e*. They differ from the pleromic elements chiefly in position, since histologically they are similar. They are, however, generally somewhat shorter

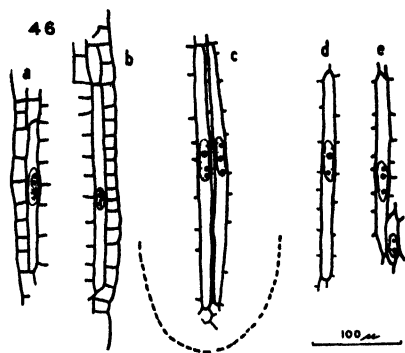


Fig. 46.—Longitudinal sections showing secretory elements from early telo-stage embryos: *a* and *b* are subdermal elements; *c*, *d*, and *e* are pleromic elements. Nuclei are elongated and have several nucleoli. Collection of June 25, 1932.

and tend to form from a series of cells, which seem to intercommunicate later by disintegration of the end walls. These subdermal elements will be discussed later in connection with photographs of late telo-stage embryos. The appearance of secretory elements in their typical form is seen in photographs of the late telo-stage embryo, Figs. 65, 75, 76, 77, 78, 79, and others; also in the germinated seed in Fig. 67.

The nature of the contents of these elements is unknown. It is possible that it might be a type of resin, mucilage or gum, or tannin or tannin product, but other possibilities are not excluded. Ordinary resin is

soluble in xylol; the marked insolubility of the dense material shows it to be quite different in this respect.

The major size increase in telo-stage occurs in the axial region of the embryo and in formation of the cotyledons. As mentioned previously the calyptroperiblem maintains its general proportions from early telo-stage. A photo tracing (Fig. 45) shows a very slightly oblique section of the calyptroperiblem at mid telo-stage. The derivation row initials at the base of the plerome and above the columnar tissue are seen to be fewer in number and more restricted than previously. This has come about through an advance in development of the tissues generally, with a relatively diminished rate of growth in the calyptroperiblem. This same group of initials at the top of the column forms the focal point for rows of cells within the plerome, but it is doubtful that they ever contribute more than a few cells at the base of the plerome in the embryo. Later on, however, they become the primary contributors to apical growth of the root, and consequently they constitute the real generative meristem of this part of the plant. No very definite organization prevails in this group of initial cells. Sometimes the rows of plerome tip cells seem to radiate from one chief cell of this group but close observation makes it evident that no one

cell can be responsible for initiating the whole of the plerome, even later on in the seedling when this meristem is more restricted. Fig. 64 shows a section similar to Fig. 45 in which the calyptrorperiblem and basal plerome are slightly more developed. The juncture zone is evident. The distance from the pleromic arc to the suspensor is about  $520\ \mu$  and the embryo is  $345\ \mu$  in diameter at the juncture zone.

Figs. 63, 65, and 66 show longitudinal sections of late telo-stage embryos which would have continued to grow for some time, chiefly in length, and at a slow rate. The major part of growth has been attained, however, and embryos of this stage of development will be used as a further basis for discussion of the late embryo. We will take up first the embryos as seen in longitudinal sections, and then the tissues more specifically with reference to the transverse sections.

Axial elongation is a process of intercalation throughout telo-stage. The periblem is composed of rows of cells which can often be traced continuously from near the base of the cotyledons down into the calyptrorperiblem below. Longitudinal growth in this tissue progresses by transverse (anticlinal) division of cells. The number of rows in the periblem appears to vary somewhat, due in part to difficulty in accurately defining the outer boundary of the plerome. The usual number seems to be five or six. Occasionally in the upper part one row splits into two by means of a periclinal division, but on the whole the cell rows of the periblem are remarkably continuous.

The plerome has arisen from a massive group of cells which originated in the pleromic centrum. The upper part of the centrum also has contributed the plumule primordium and nodal primordium and most of the cotyledons. At the base of the centrum the calyptrorperiblem and periblem have originated as previously described in the section dealing with the ana-stage embryo. The cells at the top and those at the bottom of the pleromic centrum constitute the two major centers for tissue differentiation in the embryo. The cells in the median section of the centrum finally divide in series during telo-stage to form a type of pleromic derivation row which produces the greater length of plerome proper. The derivation series of the plerome are composed of cells more elongated and narrower than those in the periblem, but fewer in number. The end members of the rows are frequently cuneiform similar to the end cells of other kinds of derivation rows. The plerome tissue may be contrasted with that of the periblem by saying that it likewise is composed of cell series, but the series are not so long and extremely continuous as those of the periblem.

Not until after germination is an endodermis visible. From the configurations of component cells seen then, and the cell alignments at present noted in the late telo-stage *Larix* embryo, it does not seem likely that the endodermis is histologically definable. It seems more reasonable to con-

sider it as a structure of physiological origin, which is not definitely predetermined in the cell rows of the embryo axis. Since the endodermis formed later is composed of large cells, histologically quite similar to the periblem cells which enclose the smaller-celled procambia, it seems likely that the inner layers of the embryonic periblem contribute the endodermis. However, more closely spaced germination stages than are now available are necessary in order to prove this point.

The medullary region is no more precisely definable in the late embryo than are the procambial strands. The medulla may be recognized by the slightly broader diameters of the pleromic cell series and by the secretory elements which differentiate within it. The nodal primordium, which seemed continuous across the top of the plerome at an earlier stage now shows a central perforation because the procambial cells are more definite. A few cells of the central medullary tissue now seem to extend into the region of the plumule meristem. This is due to the enlargement of certain of the centrally located nodal cells to correspond in character with those of the medulla. This slight change is seen in Figs. 63 and 71, and also in transverse section in Fig. 77.

Buchholz and Old (1933) have shown that the mature *Cedrus* embryo is similar to that now described for *Larix*, although the proportions of certain tissues are different. It is not to be expected that the tissues differentiate to the same relative degree in the embryos of different genera in the Pinaceae, although tissues corresponding to these described in *Larix* seem to be present in the late embryos of practically all gymnosperms.

It has been mentioned that the plumule primordium is not covered with a definite dermatogen. Fig. 71 shows a characteristic cell configuration in longitudinal section. The mantle cells are large, deeply staining, and obviously meristematic, with potentiality of division in either periclinal or anticlinal planes. The primordium is about 200  $\mu$  broad at the base and may be thought to include cells as much as 70  $\mu$  below the tip. This section shows how far the apical meristem has developed beyond the single apical cell stage. Transverse sections across the tip, as shown in Figs. 70 and 72 sometimes show a single mantellary cell occupying the apex. This arrangement is by no means constant, and the coordination of meristematic activity is not confined to any single cell more than to others in the same region. Different arrangements of the cells at the apex are shown in Figs. 73, 74, and 75.

Primary leaves originate, on germination, at the basal angles of the plumule primordium between cotyledons. Generally two or three of these may be seen before the plumule has elongated. As elongation takes place other primary leaf primordia are produced in close spiral sequence. The

general effect on the central primordium seems to be that its conical shape, as seen in the embryo, is reduced to a more rounded form.

Transverse sections of late telo-stage embryos show the radial configuration of embryonic tissues. Cotyledons are usually five or six in number. Fig. 68 shows the disparity in length previously noted in longitudinal sections. Toward their bases the cotyledons show the indefinite rounded central groups of smaller cells constituting their procambia. One of the layers of larger cells around the procambial strand later forms the bundle sheath; the others form mesophyll on expansion after germination. The dermatogen seems definite on the surfaces of embryo cotyledons, and later during germination it differentiates into an epidermis with stomates on the two adaxial sides. Stomates are first seen within the seed at the base of the cotyledons near their axils before they have elongated to any marked degree. In Figs. 70 and 75 the subdermal secretory elements are seen, usually occupying angles between adjacent dermatogen cells. (These have been inked for greater clarity along the lower part of Fig. 75.) In no case have they been seen out of contact with dermal cells either in the cotyledons or in the axis. One or two pleromic secretory elements later become associated with the cotyledonary bundles but are as yet hardly demonstrable.

The point of cotyledonary attachment is seen in Fig. 77. At this level the procambial strands are inclined outward preparatory to entering the cotyledons, and consequently the procambia are cut obliquely. Considerable difference in depth of the cotyledonary sinuses is seen, which is probably due to the same cause which makes for slight asymmetry among the cotyledons. The large-celled tissue in the center is continuous into the medullary region. Figs. 79, 69, 76, and 78 are cross sections of the embryo axis in the order given, down from the node. (Their respective positions on the different embryos selected for illustration are indicated by the diagrams on p. 85. All show pleromic secretory elements, and subdermal elements are shown in all but the lowest section, Fig. 78. The secretory elements of both kinds occur most abundantly in the central zone of the axis. The pleromic elements are more apt to be continuous; the subdermal canals are individually shorter in vertical extent though more numerous. The dermatogen is present over all the surfaces shown in the figures mentioned above. However, only on the upper portion which will become hypocotyl on germination does an epidermal layer develop fully. The lower portion of the axis will become associated with the radicle, and the outer layers of the radicle are sloughed off (see Fig. 67).

Enlargement of the axis during late telo-stage is more related to enlargement of previously formed cells than to growth by cell division. The procambial areas stain deeply, are composed of small cells, and are

more highly meristematic. The medullary area is more like the periblem in character than the procambial tissue directly outside it. The procambial strands are not yet sufficiently distinct to show a transition region, and consequently no line may be drawn as to the limits of hypocotyl and radicle.

Nearly all of the transverse sections show the embryo to be slightly flattened. This may be responsible for the frequent diarch condition in the root suggested in Fig. 69. It may be induced by the elliptical shape of the seed and gametophyte, both by pressure and indirectly because of differences in nutrition. Nevertheless, it also may have definite phylogenetic significance.

Cross sections near the plerome, the plerome apex, and juncture zone, are shown in Figs. 81, 82, 80, and 83, approximately in descending order, although sections from different embryos cannot be precisely assigned as to height in this region. In longitudinal sections the cell rows in the plerome and periblem converge toward and around the radicular plerome tip, and thus focus attention on it. However, they also give a misleading idea of its definitude. Transverse sections fail to show such a distinct separation of tissues at the tip of the plerome.

Fig. 81 is above the zone of initials at the tip and shows no precise distinction of plerome and periblem cells. In longitudinal section the periblem cells are more elongated than the central cells, but in the transverse sections these cells do not show much size distinction. The periblem cells are somewhat narrower, showing the prevalence of radial division but this is about the only difference. Fig. 82 shows a central area of considerably larger isodiametric cells within the zone of initials. Periblem cells show evidences of being sectioned obliquely as they curve down toward the columnar tissue below. Fig. 80 is very similar. Fig. 83 shows a section which crosses the juncture zone on the right, and the calypetroperiblem cells around this margin are cut more obliquely than the others. The large central cells are perhaps more properly considered as belonging to the short uppermost derivation rows of the column than to the plerome initials. They show more regularity, and the outermost cells have undergone radial division preparatory to sending off new peri-columnar series. In most of these figures just mentioned, the dermal layer is more irregular than in the sections across the axis above. In Fig. 83 the dermal layer is noticeably more variable beyond the point where the juncture zone is crossed. The line of distinction between the peri-columnar tissue and the higher rows which bend into the periblem, is of course more definite near the margin because the two tissues merge beneath the surface.

Fig. 84 is taken from near the top of the column, Fig. 85 is located in the central part of the calypetroperiblem, and Fig. 86 is at the base of the embryo. This last photograph shows the transverse configuration in the

region where marginal cells have been added to the suspensor, and the central columnar cells are still for the most part non-vacuolate. The large central cells of the column are outstanding. The much narrower radially directed peri-columnar cells afford considerable contrast, although the marginal columnar cells, divided into two by a radial wall, show clearly the transition between the two tissues. Mantellary cells are not distinguishable from peri-columnar cells except by position in transverse sections of the calypotroperiblem. Fig. 86 shows the column maintaining its individuality all the way to the base of the calypotroperiblem. Basal cells of the peri-column are apparently more readily added to the suspensor than are those of the column proper, since the suspensor regularly extends up further along the sides than it does in the central part.

#### THE GAMETOPHYTE DURING EMBRYO DEVELOPMENT

In transition from pro-stage to meta-stage, primary suspensor cells of the proembryo elongate and push the tip of the embryo system through the archegonial jacket cells at the base of the archegonium into a more or less pre-formed corrosion cavity. In *Larix*, as in pine (see Buchholz 1918, p. 195), the gametophytic tissue below the archegonium seems to break down at the regular time, whether an embryo is present or not. At least two-thirds of the gametophytes sectioned which should have contained meta-stage embryos were barren but still possessed a slender corrosion cavity, sometimes going half the length of the gametophyte. Prior to fertilization a trumpet-shaped zone of nutritive tissue appears, encircling the archegonia and extending down the middle. It corresponds with the stippled zone shown surrounding the embryo in Fig. 1. The rest of the gametophyte is more translucent. Later when the embryos are growing, the gametophyte becomes white, turgid, and packed with food, the central tissues filling first. If no embryo has been formed the gametophyte still simulates this condition. Sections of barren seeds show this to be chiefly due to a denser cytoplasmic content rather than to actual food storage; nevertheless, it is very difficult to distinguish whole gametophytes in this condition from fertile ones under a Greenough type binocular microscope.

The difference in staining properties of cross sections immediately makes it obvious which of the gametophytes contain an embryo. The safranin picro-nigrosin stain used on this material, has a strong affinity for rapidly growing or physiologically active tissue. Consequently the fertile gametophytes stain so much darker on the slide that they are at once apparent to the unaided eye. Sterile gametophytes retain only a light purple tint. In the "automatic" corrosion cavities lacking embryos, the break-down of tissue leaves a residue very similar to that formed in the old archegonia of fertile gametophytes. In fertile gametophytes this deep-staining material may be a degradation product from the early

suspensor, etc., after being acted upon by archegonial enzymes such as postulated by Stopes and Fujii (1906).

Woycicki (1923) has discussed the multinucleate cells of the *Larix* gametophyte. These were again observed during the period of early embryo growth near the central "core" of the gametophyte while the cells were filling with food. These multinucleate cells disappear later by formation of additional walls in such of them as are not disrupted by enlargement of the corrosion cavity.

The gametophytic storage cells become completely gorged with globules of food material during early ana-stage, and it is not likely that there is much physiological connection with the parental sporophyte plant subsequent to this, particularly since rapid induration of the seed coat also reduces the possibility for translocation.

As the embryo increases in size it displaces gametophytic tissue, and this seems to be the extent of the food used for embryonic development, since the cells of the gametophyte that remain out of contact with the corrosion cavity still retain their full quota of food so far as can be judged. Sometimes during ana-stage a depleted zone to a depth of a cell or two surrounds the corrosion cavity, indicating that it is not spacial displacement alone which causes the gametophyte cells to be relieved of their contents. In telo-stage fewer uncollapsed but depleted gametophyte cells are seen—generally a few can be found at the end of the corrosion cavity above the cotyledons. Only the gametophyte cells directly adjoining the corrosion cavity and the embryo are lighter-staining and have less nutritive materials than the normal quota.

The outer layer of gametophyte cells adjacent to the megaspore membrane at the base of the seed are notably different from the storage cells within. They have dense cytoplasm but very little stored food. It may be that this layer is a vestigial gametophytic epidermis. The layer is clearly visible surrounding the base of the gametophyte shown in Fig. 63, but at the low magnification used in this illustration it can be distinguished only as the narrow lighter stained margin at the top of the picture. It is a persistent structure, apparent after the gametophyte has received its full quota of food, and can hardly represent a layer of ordinary gametophytic cells as yet unfilled. It seems never to become obliterated and is demonstrable in all the late telo-stage gametophytes which were sectioned, representing a fairly long developmental period. Doyle and Looby (1939) have recently reported a similar gametophytic structure in *Saxegothaea*, and they likewise compare it with an epidermal layer. Probably it will be found rather widely distributed among the Coniferales, notwithstanding the few notations as to its presence.

The megaspore membrane is definite around the basal part of the *Larix* gametophyte, and in suitable sections its outer surface can be seen

to have a rather characteristic finely granulose texture; its inner surface is smooth. Layers, if any, are difficult to distinguish. Its thickness is inconstant, being about  $6\ \mu$  at the basal end and diminishing gradually toward the micropylar end, where it becomes either extremely delicate and probably perforate or actually wanting (Figs. 1, 47a, 48, 51, 63, 67). In preparation of sections, strips of the megaspore membrane are frequently displaced as in Fig. 73.

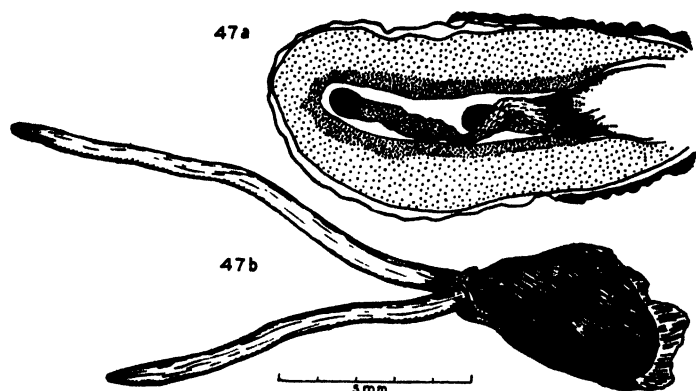


Fig. 47a.—Gametophyte containing two ana-stage embryos of about the same development, which may have been derived either by cleavage from one embryo system or from two separate embryo systems. Both embryos might have survived, since the second shows remarkably little adverse effect from its less favorable position. Magnified about 25 times. Collection of June 11, 1933.

Fig. 47b.—Germinated seed containing two viable embryos and possibly representing a situation analogous to that shown in Fig. 47a. Tips of the protruding radicles were colored a delicate pink; their surfaces showed irregularities due to sloughing of outer cell layers. No root hairs were observed.

## V. DISCUSSION

### RELATIONSHIP OF *LARIX* WITHIN THE PINACEAE

Within recent years both Doyle and Buchholz have given consideration to the affinities of members of the Pinaceae, and both reach very similar conclusions with respect to *Larix*. Earlier authors often grouped *Larix* with *Cedrus* and sometimes with *Pseudolarix*, no doubt due to the obvious resemblances of the short shoots. More recently the error in these conclusions has become a matter of general agreement. Jeffrey (1904) and Penhallow (1904) from their studies of anatomy both conclude that *Larix* is closely allied to *Pseudotsuga* and *Picea*, with *Pinus* not far removed. Doyle's studies (1918), based on the pollen, male fructification, the female cone, pollination mechanism, and the female gametophyte, are

in thorough accord with the conclusions of the wood anatomists. He is most certain of the close relationship of *Larix* and *Pseudotsuga*, notwithstanding their difference in habit, and concludes by saying "that a close natural affinity exists between *Larix* and *Pseudotsuga*."

Buchholz (1920a) groups *Picea*, *Larix*, and *Pseudotsuga* together because of their similar embryology. The similarity of the embryos of *Larix* and *Picea* is said to be especially close. The new features of embryo development in *Larix* reported in the present study, will very probably be found similar in the other two genera, although little has been reported which deals with the critical stages. In a slightly later publication (1920b) Buchholz shows *Larix*, *Picea*, and *Pseudotsuga*, together with *Pseudolarix*, as derived from *Pinus* as their closest relative. Since then the embryology of *Pseudolarix* has been studied, and Buchholz (1931) does not now consider that genus directly related to *Larix*, *Picea*, and *Pseudotsuga*.

The present work shows little additional evidence of affinity with respect to *Pseudotsuga* or *Picea*, largely because their embryogenies are not yet worked out in sufficient detail for close comparison. It does, however, tend to emphasize the substantial bond of affinity between *Larix* and *Pinus*. Whereas the two were previously considered to be quite different in having simple and cleavage forms of polyembryony, respectively, now it has been shown that the sequence is qualitatively the same. In *Larix*, the product of one embryo initial cell (as in *Pinus*) dominates its quadruplet brethren and alone contributes to the final embryo. The fact that in *Larix* the polarity units are much more closely associated in early development than in *Pinus* is significant, but this is only a difference in degree. Apical cells are similarly functional in both genera, although *Larix* usually disposes of its single apical initial earlier in ana-stage than does *Pinus*. The homologies of the structures of early embryology in these two genera are absolute throughout. All in all, this embryological study confirms the relationships currently accepted for these two genera on the basis of other lines of evidence.

#### TISSUES OF THE *LARIX* EMBRYO

*The Apical Cell in Larix*.—Schüepp (1926, p. 38) defines an apical cell as follows (free translation): "An *apical cell* is one distinguished through size, form, and manner of division, occupying the entire initial zone of a vegetative apex. All displacement curves originate from it, and all tissues of the growth segment are derived from it. At each mitosis the apical cell forms two dissimilar daughter cells, one of which retains all characteristics of the apical cell. The other becomes a segment that constitutes, either by itself or in combination with other segments, a zone of

youngest increment and becomes transformed through progressive maturation into permanent tissue."

This definition is essentially based on "formal" distinctions. To it should be added that the apical cell in order to sustain its characteristics must occupy the apex of the polarity gradient and serve as a coordination center for growth processes, in addition to the more obvious mechanical function of adding new segments.

When we regard the early embryo system of *Larix* as a compound structure, the cells at the tips of the four polarity units seem to conform in all essentials with this definition; this is also true of the homologous apical cells in pine. Apical cells in both are recognized until after the massive tip has been formed. The apical initial is longer lived in pine than it is in *Larix*, but its duration is variable in both.

The apical cells of the four polarity units in *Larix* are closely appressed, so that they conform to none of the idealized apical cell forms generally thought of. The brief stage in which the apical cell possesses three cutting faces is somewhat analogous to the tetrahedral apical cell displayed to advantage by the *Equisetum* stem tip. It is probable that this similarity is due to a mere duplication of form in a relatively simple morphologic structure organized to serve a somewhat similar function in both instances. It is believed that little emphasis should be placed on this feature as an indicator of phyletic affinity between conifers and Pteridophytes.

In *Larix* the sequence of apical cell forms is adequately explained by the mutual relations between the four polarity units which essentially determine their shape. The four apical cells originating at the base of the proembryo and enduring through the first two-thirds of meta-stage, are all more or less deformed on their faces of contact. When the apical cells grow sufficiently to cut off segments in two planes, the central angle of contact between the polarity units still occupies a large portion of one side. Only when this lateral contact has been decreased does the apical cell separate segments in three planes. It seems safe to infer from this correlation that the stage II apical cell is chiefly maintained due to the close association of the four polarity units.

Throughout the Pinaceae, so far as known, the proembryo organization is equivalent; the few cells produced in the various genera are easily homologized. *Pseudotsuga* may be an exception, since there is some doubt as to the presence of rosette cells in this genus. However, if they are absent, perhaps we may assume that the relict nuclei of *Pseudotsuga* correspond to both the rosette tier and the relict nuclei of *Larix*, in an undivided condition. Buchholz (1918, p. 201) recognized that "a distinct apical cell stage exists [in *Pinus*] from the time the embryo cells first

have walls." It is known that "Cedrus, Tsuga, and Pseudolarix have extensive cleavage polyembryony in their program of development" (Buchholz, 1931a). Of these Pseudolarix is the only one about which the existence of apical cells in the dominant group of polarity units is in question; the others all resemble pine in this respect. In their pro- and meta-stage, so far as known, the polarity units of Picea, Pseudotsuga, and Abies are very similar to Larix. Buchholz (1920b, 1926) has reported that cleavage polyembryony sometimes occurs in Abies and that otherwise it is similar to Larix. Now that Larix is known to have apical cells functioning as in Pinus (the early embryo sequence differing only in degree as to cleavage), it is most likely that these other members are similar in their possession of apical cells. Proof, of course, lies in discovering the separate proembryo quadrants functioning as individual polarity units.\*

Hutchinson (1924) apparently is in agreement with Buchholz (1920b) concerning Abies, since he recognizes what he thinks is cleavage polyembryony in "ten per cent of the cases studied." Buchholz (1926) found twelve per cent. Hutchinson's series of the embryologic sequence is probably incomplete. His meta-stage drawings can all be interpreted in excellent agreement with the sequence which has been found in Larix, although an illustration based on a single section in a series cannot be expected to provide conclusive information. It is probably necessary to base conclusions in the first place, not only on sectioned material, but on dissections as well. However, a definite overtopping by one polarity unit is shown in Hutchinson's Fig. 15, but the apical cell shown by him belongs to a repressed member. In his Fig. 16, the apical cell of an overtopping unit is shown. Since no dates of collection or discussion of the amount of material studied is given, we are led to infer from the nature of the figures that it was not extensive.

The early embryo of *Pseudotsuga douglasii* has been briefly described by Lawson (1909) and, except for some question in regard to rosette cells and the relict nuclei, shows a remarkable agreement with Larix. The only meta-stage system illustrated by him still has only stage I apical cells; consequently, similarity with Larix in later stages rests chiefly on inference supported by the observations by Buchholz.

Keteleeria has not been the subject of any published investigation of the early embryo, although Buchholz (personal communication) has observed the occurrence of cleavage polyembryony and functional apical cells in the genus. In this respect it is comparable to early stages in Pinus,

\*In *Abies venusta* Buchholz (1942) has found evidence that in some instances the four dominant polarity units may join *equally* in contributing to the single mature embryo. The manner in which these apical cells combine in these instances may have considerable biological significance and deserves a further investigation in which both serial sections and dissections are utilized.

but an important contrast is to be found in the indefinite number and continuing development of additional polarity units during meta-stage.

If the proembryo arrangement, as reported by various investigators, is of significance in postulating later development it would seem that well-developed apical cells are present in all members of the Pinaceae.

The manner of elimination of apical cells is known only for *Larix* and *Pinus*. It seems that the apical cell does not keep pace with the cells behind it in development, so that it is soon relieved of its office as a coordinator of growth processes. It does not increase in size or prominence with successive growth and is finally lost, even as a morphological structure, by subdivision either periclinally or anticlinally. In both *Pinus* (Buchholz, 1918, p. 204) and *Larix*, the embryo tips retaining an apical cell longest have a more conical shape than those which have dispensed with it earlier in ana-stage. The apical cell is retained somewhat longer in *Pinus* than in *Larix*, and the significance of this is open to several interpretations. Whether it is dispensed with because of its incompetence or whether it is eliminated in the course of subordination to a new center of embryonic organization which supersedes it, cannot be determined. Because of the association of a more or less equilateral tetrahedral apical cell with a cone-shaped apex, both in these conifer embryos and in unrelated cryptogams, it may be thought that any force which tends toward early formation of a broader embryo tip tends toward earlier elimination of the apical cell. Phylogenetic interpretation of it would seem to require some knowledge of whether ancestral plants possessed embryos with apices of broader or narrower relative proportions at a comparable stage in their ontogeny.

*The Suspensor.*—In *Larix* the primary suspensor cells function in a manner comparable to pine but *seem* to disintegrate somewhat earlier. It is possible that the suspensor cells of *Larix* are actually less stable as living structures, but comparative observations on this point have not been made with sufficient precision to establish it. Slow growth characterizes meta-stage development in *Larix*, and this is more likely a point of real distinction between *Pinus* and *Larix*. Illustrations published by Buchholz (1918) and several earlier workers show that a tetrahedral apical cell is often formed in pine after not more than four or five segments have been cut off. This is easily determined, since the embryonal tubes may be observed in connection with functional and uncollapsed primary suspensor cells. Buchholz reports that the apical cell with two cutting faces (stage II initial) is practically non-existent in pine. The segments produced by the stage II apical cell in *Larix* represent, then, just so many more meta-stage cell divisions. In *Larix* it has not yet been possible to observe the number of previous suspensor cell segments even

at the time when the stage II apical cell is first demonstrable because they are already too badly disintegrated. As a result of this, there is little information available as to the absolute number of previous segmentations of the stage I apical cell. These are not, in any event, less in number than the segmentations of the apical cell with a single cutting face in pine. Counting segments produced by the stage II apical cell as an excess over those formed by *Pinus*, it seems likely that somewhere between two and three times the actual number of segments are produced before a tetrahedral cell is formed. If we assume that each segmentation in *Larix* takes the same amount of time as in pine, the meta-stage period is necessarily also lengthened from two to three times. It appears more probable that *Larix* does *not* grow with the same rapidity as pine, because the four individually polarized units of *Larix* are developing in intimate competition. Under these conditions it would seem that the more competent members, at least, would be retarded in growth by the others. Furthermore, each of the four apical tips has less than one-half its external surface free to absorb nutriment from the outside, whereas in pine each tip is freely exposed for absorption on all but the basal surface. For these reasons the meta-stage growth may be expected to take *more* than three times as long as is required by pine. From the material at hand, the *Larix* meta-stage has been estimated to consume about thirty-six per cent of the embryonic growth period. On the other hand, the author would estimate that the stage will not be found to occupy more than six to eight per cent of the embryonic growth period in pine.

The time disparity in length of meta-stage between the two genera, will go far to explain the seeming early collapse of the suspensor in *Larix*. Enzymatic activity is not likely to be retarded commensurate with the retardation of apical growth due to competition. In *Pinus* and *Larix* the early suspensor finally disintegrates, and this may be attributed in both cases to digestive enzymes. Stopes and Fujii (1906, p. 13) report that the walls of suspensor cells in *Pinus* contain amyloid, "for in a fresh condition they stained bluish with iodine." Thus it is likely that the suspensor cells are not very resistant to digestive processes once they decrease metabolic activity in the course of maturation. It is difficult to suppose that any other agent would be active in producing the extreme decomposition found. It is, therefore, believed that the amount of disintegration of these elongated cells is a function of two factors: (1) the degree of maturity of the cells themselves, and (2) the length of exposure to enzymatic action.

The prolonged meta-stage in *Larix* may explain why older cells of the suspensor are in advanced stages of disintegration for a period before the tetrahedral apical cell occurs, while in pine they are usually found in good condition. In practical application this is almost certainly the reason the *Larix* suspensor has been reputed to collapse early, and a partial ex-

planation of why the sequence in this and related forms has previously been somewhat misinterpreted. It is impossible to understand the meta-stage growth in *Larix* by following development of the early suspensor, as has been possible in pine and some other genera, because the older cells always disintegrate while the tips are in an unadvanced stage of development.

Data recently presented by Buchholz (1942) indicate that the primary and early secondary suspensors of *Abies* are more like those of *Larix* than are those of *Picea*. The two meta-stage embryo systems of *Abies* shown by Hutchinson (1924, Pl. XVIII, fig. 8) illustrate the difficulty in tracing the suspensor cells at this time, especially from sectioned material. From study of *Larix*, it seems very likely that the tips shown in his Figs. 10, 12, 13, 14, 15, and 16, each represent four polarity units. Each group would in such a case be derived from a single archegonium, and represent an embryo system. Hutchinson did not recognize the compound nature of these groups consisting of "four chains of cells."

After the embryo tip becomes massive the suspensor of *Larix* appears to agree closely with that of the late embryo of pine. The cells of the massive suspensor are derived for the most part from more specialized cells at the base of the columnar tissue. They differ from the embryonal tubes of meta-stage in length, becoming less than a third as elongated. The suspensor is nearly as large as it ultimately becomes at the end of the ana-stage, and very few cells are added to it after early telo-stage. At germination only a collapsed and partly "jellified" mass remains, and this is immediately sloughed off in exit from the seed.

*Tissues of the Mature Embryo.*—It has been generally recognized since Strasburger's investigations, and even before (cf. Buchholz, 1918), that the plerome apex could be distinguished first, next the plumule primordium, and lastly the cotyledons. These are all features which may be observed in gross dissections; but beyond these particulars, little has been known as to the origin of embryonic tissues. Strasburger's figures, which are the most complete that we have, are frequently taken from entire embryos and drawn as optical sections. To the author these appear too definitely symmetrical and too precisely differentiated to be taken as representing the actual condition. Comparative study of tissue origin may furnish significant differences between the various conifer embryos if it is ever adequately investigated, but these differences will be chiefly quantitative rather than qualitative.

Whatever the sequence and origin of the embryo tissues may be throughout the Coniferales and Gymnosperms in general, we do have considerable accurate information of tissue configurations in the later stages. Growth processes are slowing down at this time and only differences in degree of development take place within tissues previously formed. Sections are more easily obtainable from the large embryo, and

mature seeds in a general way have been objects of a relatively large measure of scientific interest. The tissues of all or nearly all mature gymnosperm embryos may be enumerated in detail as follows: massive suspensor; column and peri-column; a region of generative initial cells at the basal tip of the plerome; periblem; plerome; cotyledons; a dermal layer of varying distinction; procambial tissue of varying prominence; medullar tissue more or less definitely defined; a plumule primordium of varying development; an embryonic secretory system which is probably present in many late embryos but has frequently been overlooked.

There are seen to be two active meristematic regions; one at the base of the plerome and one at the cotyledonary end of the axis. The basal region of initials gives rise to columnar tissue which is instrumental in forming the peri-column and periblem. This is accomplished by a direct alteration in polarity of the outer cell rows in the column. In transverse sections the columnar cells contrast greatly with the peri-columnar cells in size. Apparently this transverse appearance led Hutchinson (1917) to mistake the column for the lower part of the "axis" extending through the calyptroperiblem in *Keteleeria*. Even in longitudinal sections the line of division between the peri-column and the columnar tissue is one of the most sharply distinguished in the whole embryo, especially when the protoplasmic contents of the cells are observed, since these usually give indication of the cellular polarity. Mere outlines of the cell walls in longitudinal section minimize this line of distinction. However, it must not be inferred that this or any other embryonic tissue is precisely demarcated along its border, because any individual border cell of the embryo is functionally plastic, adapting itself to the local tissue development.

The most remarkable development which takes place is the contribution of peri-columnar tissue to the original periblem. Previously no one has given much consideration to the origin of the periblem, or the mechanism for lateral growth in the embryo. It seems to have been assumed that the periblem originated by periclinal division of cells in the axial region. The obvious cell row alignment between the periblem and upper part of the peri-column was explained by Chamberlain (1935, p. 267): "Of course the root cap comes from the lower layer of meristematic cells and so it is said to come from the periblem." Chamberlain also stated (p. 270): "Practically all authorities say that the root cap comes from the periblem." He made no distinction between column and peri-column, and he retained the term "root cap" for these two tissues, although Buchholz and Old (1933) had clearly shown that there is no root cap in the conifer embryo comparable to the structure in angiosperms or ferns. The term calyptroperiblem, which they proposed to include the two tissues herein designated as column and peri-column, is a desirable terminological distinction. The sequence in *Larix* shows that

the periblem instead of contributing to the calyptroperiblem is really originated from it. Once formed around the plerome the periblem is self-perpetuating in the embryo, since it increases in length by intercalary growth. Young seedlings have shown the periblem of the radicle to be maintained in early growth by additional contribution from the pericolumn. As Buchholz and Old have indicated, there is no break whatever in the cell rows from the pericolumn into the periblem. In development of the embryo tissues (mid ana-stage), cells located in the uppermost pericolumnar region produce progeny whose relative position changes until they are in the periblem zone; in the course of growth in length, these original periblem cells multiply along with the pleromic tissue but without further addition of cells from below.

The real generative region of the root lies nearly exclusively in the group of large, nearly isodiametric, initials above the column at the basal tip of the plerome, no distinction whatever being possible between the initials contributing to the two, except their general position in this generative meristem. As we trace rows from the lower part of the periblem in the embryo, down into the pericolumn, the number of pericolumnar rows *increases*. In tracing cell rows in the plerome downward the number of rows *decreases*, and all rows converge toward the generative initials. However, in the embryo only the basal part of the plerome is derived from these initials, as those above come from the central zone of the original pleromic centrum. In the seedling, all root growth originates from the generative initial cells, both above (for the plerome), and below (for the column, pericolumn, and periblem). The plerome and periblem, while coming to lie side by side, are for the most part actually derived from the top and lower margins, respectively, of this one generative meristem.

The relations of the upper tissues are about as has been previously considered. The plumule primordium has long been known to lack an apical cell and requires no special discussion. The "nodal" meristem is the first of the procambial structures to become recognizable, and in *Larix* it is the region in which tracheids first appear after germination. The cotyledonary primordia contain procambial branches continuous from this nodal region from a very early time. Pleromic procambia are not very strongly differentiated until later telo-stage.

According to the embryologic concepts of Bower and Lang, the root in pteridophytes is to be considered as a lateral organ. It is, therefore, a point of considerable phylogenetic importance to note that the primary root, as developed by gymnosperm embryos, is in every sense axial in formation. The first radicular formation is the columnar tissue developed early in ana-stage, which later becomes narrowed, by lateral sapping, to become the column. After germination this structure gradually diminishes

in prominence. Still it is an important constituent of all gymnosperm roots, since it is the immediate source of protective tissue below and around the delicate generative initials. It originates *de novo* on the secondary roots. Although certain histologists, and among them Schuepp (1926) have attempted a more or less formal classification of root "types" and have included some angiosperms in the same type assigned to gymnosperms, it is doubtful whether more than a superficial similarity exists between the two groups. It is a significant point that all gymnosperms are admittedly similar in root tip organization. The strictly axial derivation of the root in gymnosperms, a structure *set-in* between the apical meristem and the suspensor, is thought to be of particular significance, as will be brought out in the discussion to follow dealing with the primitive spindle concept.

#### THE PRIMITIVE SPINDLE AND PHYLOGENY

*Polarity and Polyembryony.*—Polarity is the primary consideration in Bower's "primitive spindle" concept. In the study of the *Larix* embryo particular attention has been paid to the manifestations of polarity, since this seems to be a most significant attribute of the embryo organism. All higher organisms are known to possess a major polarity gradient and subsidiary polarity gradients in their appendages. The unity manifest in this way is one of the fundamental considerations to be taken into account in defining an organism, since it is directly concerned with organization and subordination of the component parts. Polarity is largely associated with the coordinate functioning of the organism.

Coniferae are distinct among higher plants not only in the free nuclear divisions of the zygote (which is common to practically all gymnosperms), but also in frequently producing from a single zygote a number of embryonic units, each organized individually so far as polarity is concerned. *Araucaria* is an exception in that simple polyembryony is assured by a special sheath of cells, but I think this probably is a derived condition. *Sciadopitys*, on other grounds held to be fairly closely related, shows an extreme number of units which manifest an individual polarity, and *Araucarian* simple polyembryony bears slight resemblance in early stages to primitive simple polyembryony of cyads. The Pinaceae show a large measure of conservatism in regard to the number of polarized units produced by each zygote, since these seem to be relatively definite in number for each genus. The number of cells in the proembryo of each (the time at which embryonic polarity gradients are first established) likewise appears to be fairly constant throughout the group. Other conifers in the various families often show a long period extending well into meta-stage, during which new units of individual polarity are constantly being organized, and the number is often indefinite, although it is always improb-

able that more than one normally organized polarity unit will succeed in forming a functional embryo.

As a means of distinction between groups like the Pinaceae and groups in which the dominant polarity unit may be long delayed in forming or show fragmentation and "indecision" after the pro-stage, we may say that embryonal polarity in the pine family type is *pro-determined* and in the others is *meta-determined*. Specific instances need not be cited, but it can hardly be overemphasized that the time at which the final dominant polarity unit becomes established is of comparative importance. The Pinaceae are conservative in respect to the definiteness with which polarity units are produced. Furthermore, among the Coniferales, typified as they are by complex polyembryony, the relative uniformity in number of polarity units produced in the pine family is very remarkable.

For reasons elaborated in the discussion later, it is held that simple polyembryony is probably the primitive type in gymnosperms as in all other plants in which several embryos are formed by one gametophyte. At present the simple polyembryony of cycads is thought of as chiefly a size elaboration from the primitive condition. However, simple polyembryony in Araucaria is probably a derived condition made possible by the peculiar sheath of cells enveloping the proembryo group of initials. Simple polyembryony, which has been more or less conclusively demonstrated in a few other modern conifers, probably is likewise coenogenetic. Late establishment of the dominant polarity unit during meta-stage is more characteristic of modern conifers as a whole than the pro-determined condition shown by the Pinaceae. The regularity with which units showing separate polarity are established, as in the Pinaceae, probably signifies that this is a conservative characteristic, intermediate in character between primitive simple polyembryony and the advanced type of cleavage polyembryony with late meta-stage or even early ana-stage determination of a dominant polarity unit.

While the paleontological information available does not permit us to reconstruct a very satisfactory phylogeny for modern conifers, it seems very likely that, as a whole, they represent a natural group of single derivation which, among other things, was characterized by a particular tendency toward formation of many polarity units from each zygote. The ramification of the branches from the ancient source, and hence the true interrelationships of the living conifers, presents a more complex problem. The question as to which of the living genera is most primitive, seems largely academic unless fossil representatives can be cited. Nevertheless, the embryologic stability of the Pinaceae, insofar as we know the details of the intricate type of polyembryony found there, gives reason to believe that this is a relatively ancient type of embryogeny which endured with comparatively little change, while greater variation took place

in other organs. The reverse may have been true in other coniferous lines; e.g., *Thuja* and *Biota*, which show distinct differences in their early embryology, but have been considered quite closely related on the basis of vegetative characters.

*The Primitive Spindle Concept.*—The chain of thought indicated by the above title goes with chief credit to Professor Lang of Manchester and to Professor Bower, long associated at Glasgow. To the author's knowledge it is today the only fundamental concept which is comprehensive enough to be applied to plant embryology for the purpose of wide comparative analysis.

The underlying basis for the line of reasoning embodied in it may be obtained by reading Lang's essay on the ontogenetic (homologous) theory of alternation of generations (Lang, 1909). He states (p. 7) that "we are justified in assuming . . . that each stage in the ontogeny is determined by the preceding stage." He suggests a theoretical explanation for the differences in structure of gametophyte and sporophyte, largely by their "environmental" conditions which precede mature development. If we follow Lang, we must regard many of the characteristics of the embryo as being due to internal gestation of the zygote. Bower (1935), who favors an antithetic view of alternation, points out (p. 519) that "whatever the history of its origin (i.e., either homologous or antithetic), the biological importance of this internal embryology for land-living plants may be estimated from the constancy of its recurrence." By way of definition he says (p. 519), "It is to the early stages of the encapsulated sporophyte that the term 'embryo' is applied."

Lang (1915) further argues for the causal analysis of embryology in his Presidential Address before the British Association. Primary emphasis is placed on the inadequacies of what he calls the "phyletic period" of botanical science due to application of formal, or idealistic concepts. One very evident break with this mode of reasoning seen in modern botany is recognition of many parallel lines of evolution rather than the earlier strict monophyletic interpretation of the plant kingdom as a whole. The parallel lines may be presumed to have united during some ancient period, but in few instances is compelling evidence available to indicate the actual points of contact.

It seems well to point out that a more or less "formal" philosophy is required in order to have some "yardstick" for the proportional evaluation of facts, whether or not these facts are matters of formal or causal interpretation. However, it is perhaps not contended today that any purely formal interpretation should be upheld, and there is great diversity of opinion as to just how far a causal philosophy is useful. If causal precepts were carried to an extreme, the great advantage of "formalistic" generalization seemingly would be largely lost. The "primitive

spindle" concept, thus designated by Bower (1922) seems to be based on the causal reasoning of Lang to a large extent, augmented by Bower's particularly wide personal familiarity with the pertinent facts. If rigidly adhered to, the "primitive spindle" may become as burdensome as any other formal generalization. But with judicious application it would seem to render many diverse features of embryos to some extent explicable and at least logically comparable on a common basis.

The most simple example of a primitive spindle may be demonstrated in algae where the plant is related to a solid substratum. Organization of an axial polarity gradient very plausibly may have had its beginning in some such environment as this. At a further stage, Bower (1935, p. 520) says, "The retention of the egg in the venter of the archegonium would fit well biologically with the departure of the organism from aquatic life, and insofar it would accord with the correlation of archegoniate alternation and the establishment of a land flora." In all seed plants and many lower plants the apical pole of the embryo is directed inward (endoscopic). In accord with their primary polarity, Bower (p. 524) points out that "the embryo will assume at first a more or less spindle-like form, though this may be variously modified or disguised." Bower has emphasized that polarity is evident from the first segmentation of the zygote. Although this apparently holds true for all other plants above the Thallophyte level, and for most Thallophytes as well, it does not apply precisely to gymnosperms.

In establishing the "primitive spindle" concept, Bower draws upon his extensive knowledge of pteridophytes and arrives at essentially the following conclusions: (1) In all archegoniate plants, definition of polarity is the first step in development. (2) Possession of a suspensor is a primitive feature which has been obliterated in many forms; when it is present, the embryo is always endoscopic, as if the suspensor served to anchor the direction of polarity. (3) The embryonic apex has a definite relation to the first segmentation of the zygote, since it originates at or near the center of the epibasal hemisphere. (4) The leaf-formation always arises from the epibasal hemisphere. (5) The root is constant in originating as a lateral appendage in all pteridophytes that have a suspensor, although when no suspensor is present, it may *appear* to oppose the axis of the whole embryo. The root is accessory to the spindle and variable both in position and in the time of its definition.

Partly on the basis of Bower's earlier treatment (*Origin of a Land Flora*, 1908), Lang (1915) formulated these conclusions: "(1) the primary importance of the longitudinal axis of the shoot, the position of the first root and the foot being variable; (2) the constancy of the position of the stem-apex near the centre of the epibasal half of the embryo; (3) the probability that embryos without suspensors have been derived

from forms with suspensors, without any example to the converse change. These and other related facts seem to find their morphological explanation in the shoot of the sporophyte being the result of the elaboration of a filament."

*Application of the Primitive Spindle Concept to Gymnosperms.*—The question now at hand is the degree to which the embryo of *Larix* and other gymnosperms, conforms with these findings based on the vascular cryptogams. From such consideration on the basis of embryology it may be possible to reach a conclusion as to the relative degree of relationship between the two groups. The points previously summarized from Bower are discussed in order.

(1) Segmentation of the zygote: In common with nearly all gymnosperms, *Larix* shows an intercalated free nuclear phase after zygote division which precludes an immediate manifestation of zygotic polarity. It might be contended that the movement of the nuclei to the base of the archegonium is an indication of polarity, but this is more plausibly explained as being caused by factors affecting the archegonium as a whole and not as a characteristic of the nuclei themselves.

We may best designate the earliest appearance of polarity by retrospective observation. The polarity units have been defined primarily on their individual capability to form a recognizable embryo. The first definite polarity indication of these embryo-forming units in *Larix* and others of the Pinaceae is observed in the last cell division within the proembryo. This segmentation of the apical tier perhaps may be regarded as functionally equivalent to primary segmentation of the zygote in vascular cryptogams.

A great contrast hereby obtains, which is just as characteristic of gymnosperms as a group as is direct spindle formation in the vascular cryptogams. We may conclude with little hesitation that the primary embryonic polarity in gymnosperms is delayed in its appearance, whether simple polyembryony results (as in cycads) or complex forms of polyembryony occur, as in conifers.

(2) The gymnosperms all possess a highly developed suspensor which is practically universal within the group. If we grant that the suspensor is a primitive embryologic feature we must add that it has also been a feature of specialization in gymnosperms. It has presumably endured throughout the history of this whole division of the plant kingdom. The fossil embryos of Araucarians (Darrow, 1936) and Bennettitaleans (Wieland, 1916; and others)\* both show evidences of the gymnospermic suspensor in their radicular conformation. Coulter and Chamberlain (1917) think Bennettites may have had a short suspensor similar to Ginkgo.

\*Although reports of embryos of other groups of fossil plants have appeared and it is possible that some are present in American Carboniferous coal-ball material, nevertheless except for the two groups cited above, there is no information as to the characteristics of fossil embryos yet available.

The first cell of a polarity unit to elongate is quite comparable to the suspensor of certain eusporangiate ferns. The relatively enormous multiplication of suspensor cells, found in all gymnosperms, whether simple or not in their form of polyembryony, has almost no counterpart in the rest of the plant kingdom. It is altogether probable that in this group of plants where embryo competition is keen, the suspensor serves as a means of eliminating the less vigorous units. In *Selaginella* where a comparable case of simple polyembryony occurs, the suspensor is never of this elaborate sort, and competition evidently is not the acute and significant phenomenon that it is in gymnosperms. It may be tentatively suggested that the effect of the seed habit in modifying the organization of the gymnosperm gametophyte has conditioned the occurrence of embryonic competition.

The ubiquity of the specialized suspensor in gymnosperms requires no further elaboration in order to contend that this agrees very well with Bower and Lang's conclusions. For gymnosperms the suspensor certainly is a fundamental embryonic organ. Its mammoth development may be explained on the basis that this is the only group of plants where such an organ became useful as a dynamic means of embryonic selection and survival.

This last statement cannot be demonstrated by study of any individual modern species, and Goebel (1933, p. 1819) has expressed some skepticism that the embryos eliminated in the process of selection are as a matter of fact "unfit." If the suspensor is a primitive structure, discernible perhaps in the plants which formed the first land flora, and if the gymnosperm suspensor can be thought of as being directly derived from those possessed by some of these fundamental land plants, then we also see how it may at the present time be difficult to *demonstrate* an "unfitness." The suspensor long ago became perfected in essentially its present setting (the fossil Bennettitalean embryos prove this), and the more obviously unfit embryos have become so "weeded-out" since its effective establishment, that the unfitness of any repressed embryos may no longer be expected to show phenotypic indications. As a factor which has influenced long-term evolution it is probably none the less important.

*Larix* has shown us an easily demonstrable case where the elimination of the *less favored* (rather than the unfit) is occurring constantly. It has been demonstrated that as a frequent occurrence two of the polarity units are smaller than the other two, primarily due to an unequal segmentation of the base of the archegonium by the free nuclei. It is becoming more evident that the archegonial shape may be the chief determining factor in favoring certain of the polarity units (see Buchholz, 1941). The suspensor in such a case is still the means of elimination of the extra embryos. Since, as Goebel points out, it tends to eliminate chiefly

the slower-growing members, the writer believes that the suspensor can also be interpreted as a means of maintaining a certain standard of vitality for the race. This is justified when viewed in a perspective commensurate with the age of the group through geological eras. There are many features of organic evolution which are not objectively demonstrable from living organisms but which are real and important factors during a long span of geologic time.

(3) The gymnospermic embryology seems entirely consistent with the embryology of cryptogams in respect to the epibasal segment producing the stem apex, particularly if the polarity unit is considered equivalent to the primitive spindle. On this basis, the embryonic apex retains its definite relation to the "epibasal" segment. Delayed organization of polarity in gymnosperms, due to free nuclear division of the zygote, makes this comparison less precise than might be desired. However, rather close comparison may be made between an early polarity unit of the pine type (see Buchholz, 1929, p. 369), with the elongated early embryo of *Danaea* or *Macroglossum* and of at least one species of *Angiopteris* (Land, 1923). The epibasal cell in the latter is, no doubt, quite comparable with the early embryonic apical cell in such gymnosperms as show individual filamentous polarity units. When the embryos in these groups are thus brought into parallel, it may be admitted that the comparison is favorable. However, when the massively organized polarity unit in cycads is considered, the formal resemblance fades, although a functional comparison is still tenable. Of all the gymnosperms which are accurately known, the Pinaceae seem to offer the best material for comparison of the primitive spindle and polarity unit.

(4) The difficulty in delimiting the gymnospermic embryos as to hypobasal and epibasal portions also limits the precision with which comparison may be made as to position of the leaf-formation. Still, if we consider the axis of polarity and think of the apical pole as corresponding to the epibasal portion of the cryptogamic embryo, it is true that location of the leaf-formation (cotyledons and plumule in gymnosperms) both in gymnosperms and vascular cryptogams is in close agreement.

(5) With regard to the lateral origin of the root held to be characteristic of vascular cryptogams according to the primitive spindle hypothesis, gymnosperms show a distinct lack of agreement.

It has been shown in *Larix* that the root originates through development of a basal center of polarity produced within the original axial polarity gradient. The primary root is a structure intercalated in the primary axis as a constant feature, in direct alignment above the suspensor. No suggestion may be found of any different mode of origin for the primary root throughout all gymnosperms. It cannot in any way be considered lateral to the primary polarity gradient. Here then is a point

of fundamental distinction between the vascular cryptogams and the gymnosperms. Whereas in the former "the root is accessory to the primitive spindle and variable both in position and time of its definition," so far as I am able to see, the exact reverse is true with respect to the root in the entire gymnospermic phylum. This may likewise be true in angiosperms.

Certainly the extreme conservatism of this feature in gymnosperms is a matter of far-reaching phylogenetic significance. The root is known to show many conservative features in its later organization, but its conservatism as to place of origin with reference to the primary embryonic polarity has not been sufficiently emphasized.

If the suspensor is a fundamental embryonic organ, the root in gymnosperms is almost equally fundamental, since the suspensor and root are so intimately associated. From their relationship it seems plausible that the root became established as an invariable plant part from the time of origin of this lineage. Certainly it is one of the strongest arguments for a monophyletic derivation of the gymnospermic phylum as a whole, and it may possibly apply to a larger group of seed plants.

The conclusions Lang enumerated have also been covered by previous discussion (p. 72). Both Bower and Lang are in essential agreement as to the significance of the "foot" in cryptogamic embryos. Bower (1935, p. 542) states that the "foot" in cryptogams is essentially an "opportunistic growth." It is the one organ of cryptogamic embryos which has no counterpart in gymnosperms. The points brought out thus far are summarized in the following comparison of modes of embryo formation:

<i>Vascular Cryptogams</i> (Primitive Spindle)	<i>Gymnosperms</i> (Polarity Unit)
1. Direct spindle formation following first segmentation of the zygote.	1. Delayed organization of polarity units as a result of free nuclear division from the zygote.
2. Suspensor held to be primitive on theoretical grounds, but has suffered reduction and elimination in many of the advanced forms.	2. Suspensor a prominent feature throughout.
3. Embryonic apex has a definite relation to the first segmentation of the zygote.	3. Embryonic apex is constant as a feature associated with the apical end of the polarity unit.
4. The leaf-formation always arises from the epibasal hemisphere.	4. The foliar organs are always derived from the apical pole (= epibasal region) of the polarity unit.
5. In all pteridophytes which have a suspensor, the root is lateral in origin; it is concluded that the root is an accessory of the spindle both in position and in time of origin.	5. All gymnosperms have the root as a constant axial addition, formed in continuation with the suspensor. In no sense is it lateral to the polarity unit in origin.

Points 1 and 5 are in serious conflict; agreement seems reasonably close for the other three.

It should be emphasized in this connection that there are also other points just as fundamentally important in comparison of these great

groups of plants as the mode of embryo formation. One of the most cogent of these is that archegonia, identical in functional import, are characteristic of both.

*Comparison of Cycad and Conifer Types of Polyembryony.*—Here an analysis is attempted of the factors which have produced the greatest embryonal difference that is seen in the gymnosperm phylum, i.e., simple polyembryony of the cycad type vs. complex polyembryony of the conifer type. In this connection an explanation for delay in organization of primary polarity in gymnosperm embryos (viz., the origin of the free nuclear stage) will be considered first. It is believed that the explanation given by Chamberlain to explain free nuclear division in cycads will also account for late organization of embryonal polarity for gymnosperms in general; at least it serves as a medium for theoretical interpretation.

Chamberlain (1935, p. 142) briefly restated the idea he had previously given in 1919, viz., that the free nuclear division of the zygote may be due to the incompetency of the first small daughter nuclei to span the archegonial cavity and immediately segment the enormous cycad egg cell. The writer is inclined to accept this as a general but fundamental explanation for the widespread occurrence of this type of free nuclear division. However, the large archegonium and egg cell is not limited to cycads but is a general characteristic feature of the whole gymnospermic phylum. *Sequoia sempervirens* is the only gymnosperm known in which the egg cell is immediately segmented following zygotic division. Here the egg cell is very small in comparison with those of the other members of the phylum, and as an exception to the usual order serves to substantiate Chamberlain's causal deduction. The small archegonia probably are coenogenetic in origin, and typical compound embryony is maintained in *Sequoia*, notwithstanding the unusually early segmentation (Buchholz, 1939).

The origin of the enlarged egg cell is the point for consideration if we admit its size to be the primary necessity for free nuclear division of the zygote and consequent delay in expression of polarity. The essential agreement of gymnosperms in this characteristic is a point emphasizing the primary interrelationship of the whole group. To the writer it seems tenable to associate development of the enlarged egg with the origin of the seed habit in the gymnosperms as a response to the then newly established nutritive relations. Perhaps at that time it represented a type of nutritional "hypertrophy." While the gymnospermic archegonium shows the fundamental derivation of the group from archegoniate ancestry, still nowhere in the modern free-sporing archegoniates do we find any comparable and consistent enlargement of the egg cell. The greatly enlarged egg has all the indications of being associated with intraseminal nutrition

which must have been a new problem in organization for the original archegoniate ancestors. As yet this is almost entirely a matter of theory, although it is possible that direct paleontological evidence will some day be available.

Fossil gymnospermic archegonia have been illustrated by Brongniart (1881) in seeds from the late Upper Carboniferous (Stephanian) of Grand Croix in central France. Not only are these archegonia already much larger than those of cryptogams, but they are round to flattened ovate in shape—surely an indication that extremely elongate archegonia are not primitive in gymnosperms.\* Measurements of archegonia have been made directly from Brongniart's figures and, except in cases where the magnification was slight or as otherwise noted, are probably accurate within 20-30  $\mu$ . These measurements are as follows:

	Archegonial Axis	Transverse Dimension
<i>Cardiocarpus sclerolesta</i> (Pl II, fig 2)	300 $\mu$ 250	550 $\mu$ 425
<i>Cardiocarpus angustodunensis</i> (Pl III, fig 8)	466 666	733 746
<i>Cardiocarpus tenuis</i> (Pl V, fig 5)	400 300	900 825
<i>Leptocaryon avellana</i> (Pl VI, fig 7—including neck?)	500	550
<i>Rhabdocarpus subtunicatus</i> (Pl X, fig 20—magnification too small for accurate measurement)	666 $\pm$ 100	700 $\pm$ 100
<i>Rhabdocarpus conicus</i> (Pl XI, fig 4—"central body" may be a cordaitalean pollen grain, archegonium (?) broken, measure- ments doubtful)	240?	300?
<i>Rhabdocarpus cyclocaryon</i> (Pl XII, fig 2—measurement of "central body", archegonium proper is larger)	293	400
<i>Sarcotaxus avellana</i> (Pl XIII, fig 3—magnification too small for accurate measurement)	266 $\pm$ 50	333 $\pm$ 50
<i>Taxospermum gruneri</i> (Pl. XV, fig 5)	500	516
<i>Stephanospermum akenoides</i> (Pl. XVI, figs 4-6)	250?	320?

To give some perspective for comparison with these measurements and those recorded for the archegonia of the various modern gymnosperms, illustrations given by Smith (1938) of various cryptogams were also measured, and some of these are tabulated below. Since the arche-

\*Doyle and Looby (1939) have, however, interpreted the phylogeny among podocarps in converse fashion with regard to archegonial shape

gonia of cryptogams have an essentially isodiametric venter only one measurement, the transverse dimension, is recorded.

Genus	Archegonia	Genus	Archegonia
Azolla (p. 362).....	43 $\mu$	Equisetum (p. 245).....	66 $\mu$
Onoclea (p. 347).....	46	Isoetes (p. 215).....	79
Marattia (p. 336).....	93	Selaginella (p. 191).....	43
Gleichenia (p. 305).....	49	Lycopodium (p. 177).....	54
Osmunda (p. 292).....	58	Tmesipteris (p. 157).....	121
Marattia (p. 281).....	58	Various mosses.....	44-80
Ophioglossum (p. 273).....	102		

These measurements suffice to show that an archegonium in excess of 100  $\mu$  in transverse diameter must be regarded as exceptionally large in the cryptogams. In gymnosperms, on the other hand, an archegonium not in excess of 100  $\mu$  diameter (e.g., *Sequoia* and *Sequoiadendron*) must be considered unusually small. Those of *Larix* approximate 300  $\mu$  in their shorter transverse diameter, and cycad archegonia frequently exceed 1 mm. Archegonia of *Dioon edule* measure as much as 1,300  $\mu$  transversely and 3,800  $\mu$  axially. Of course, simple linear measurements of such bodies do not adequately express the actual differences in volume, since volume is a function of three diameters. Thus, it appears that gymnospermic archegonia so far exceed the size of those ordinarily encountered in cryptogams that this fact must be accorded some significance. As ubiquitous as this archegonial gigantism is among the different gymnospermic families, it may perhaps be regarded on the whole as a primitive and relatively conservative character. In fact it may have arisen as a direct result of attainment of the seed habit in this particular line and have its origin as long ago as Lower Carboniferous or Upper Devonian times. There is no reason to assume that a sequence of archegonial enlargement is obligatory in development of the seed habit, but in this particular division the two processes may have been causally linked in evolution.

As in all other archegoniate plants, each egg in the original gymnosperm stock very probably produced a single polarity unit, or "primitive spindle," immediately following the first egg segmentation. When the mechanical features suggested by Chamberlain became acute, due to egg enlargement, the direct establishment of polarity was no longer physically possible and various artifices were invented to serve the embryologic function. Such reasoning entirely complies with Lang's assertion that "each stage in the ontogeny is determined by the preceding stage."

There were two chief methods which could have been used in overcoming the physical difficulties brought on by the "hypertrophy" of the egg: (1) the production of a large number of nuclei which were together capable of effecting subdivision (segmentation) of the egg cavity; or (2) the aggregation of a fewer number of nuclei in a narrowed portion of the chamber and segmentation of this portion only. In the first alternative, the free nuclei would have been more likely to function in a coordi-

nate manner in forming the first embryonal tissue. By so doing they could have attained the degree of coordination necessary for rapid establishment of an embryonic unity typified by a single polarity gradient. In the second alternative, nuclear interrelations may be thought of as less obligatory with proportionally less embryonic unity being attained in the process. These might be the extreme manifestations as induced by the enlarged egg cell. Various degrees of compliance may, of course, be cited among modern gymnosperms which have, in fact, suggested the alternatives just given. The justification for extrapolating features of modern plants is that the features under consideration are fairly conservative, and there is no conflict with available fossil evidence.

In this discussion, Ginkgo is included with the cycad type of embryogeny, although it does not have the competitive features of polyembryony so markedly exemplified. Ginkgo illustrates the extreme form of archegonial subdivision by a great number of free nuclei, and as a result attains coordination of a massive embryo relatively early. The cycads are variable in the degree to which they partition the archegonium, but are essentially similar to Ginkgo in regard to formation of a single coordinated polarity unit from one egg. Both approximate fairly well the condition in free-sporing plants, where a single polarized spindle is produced, except that the proembryo is enormously more massive; by functional standards they are less diverse. Thus, Chamberlain's conclusion (1935, p. 144), that Ginkgo and the cycads show "the type of embryogeny which we should regard as the most primitive [among gymnosperms]," is wholly justified.

Biota, *Sciadopitys*, and certain podocarps (cf. Buchholz, 1929, 1931b, 1941) are examples of the complex type of polyembryony in conifers. Their mutual relationships are still largely speculative. Although it is likely that they are not very closely related, they all have a general indefiniteness of cellular organization in the proembryo which apparently is considerably influenced by the shape of the archegonial base. Always a few proembryo cells enjoy a positional "favoritism," and none of these cells represent actual polarity units. The prosuspensor, a specialized but independent embryonic mechanism, is functional in all three genera. It serves to move the apical group of cells into the corrosion cavity. There the polarity units originate out of the "favored" group of apical cells, more or less directly. All this intervening process delays definition of the polarity units, affording strong contrast with the cycad sequence. The marked lack of coordination and the indefiniteness with which the meta-determined polarity units are "selected" is characteristic of many of these more advanced Coniferales. The Pinaceae seem to have a somewhat comparable multiplicity of polarity units, but these are both pro-determined and usually definite in number, features more primitive in degree according to the criteria advanced here.

The proembryo organization of *Araucaria* is not so easily reduced to either alternative previously outlined. There, apparently another mechanism is exercised for filling the egg chamber. It cannot be conclusively stated that this is a feature of recent adaptation, but it would seem to be most satisfactorily regarded in this light for the present. The polarity is certainly pro-determined, but not until about 32 free nuclei have formed walls and organized a group of sheath cells radiating from and enclosing the embryonic group to fill the archegonium. If the suspensor-like proembryo sheath is not a coenogenetic adaptation to produce proembryonic unity, then *Araucaria* shows a third alternative method of coping with the enlarged egg cell. It seems most reasonable to hold the araucarian early embryo as derived from a complex embryonic type, at least until more evidence can be secured.

Briefly recapitulating, then, cycads and Ginkgo are thought to have met the problem of the enlarged egg cell by numerous free nuclear divisions which coordinate in formation of a massive proembryo. In these, the pro-stage and meta-stage elaboration found in conifers has been omitted, and embryologic sequences of this type are the most primitive to be found among modern gymnosperms. The Coniferales are characterized by complex forms of polyembryony. Simple polyembryony in this group is most probably a derived condition. Pro-determined polarity units are not characteristic of the group as a whole, and where they occur likely indicate primitiveness.

Since this study is not primarily concerned with gymnospermic phylogeny, the considerations given above will not be amplified. It was thought desirable to sketch them briefly since, among other things, they show the value of recognizing the basic units of complex embryology found in conifers and gymnosperms in general.

## VI. CONCLUSIONS

Apical cells are present in the early embryo of *Larix*, and the early sequence is similar to pine in its essentials of development. The four vertical rows of the proembryo are not originally equal but show the result of positional "favoritism" at the base of the archegonium.

Only one of the four apical cells of the proembryo contributes to the mature embryo, although these initials do remain united during early development. Potential embryo-forming units are designated as polarity units. Three of the polarity units are often repressed and overgrown by the fourth, which continues forming a massive embryo. The massive growth of the dominant embryo in all cases seems to be organized from the progeny of only one apical cell.

The embryogeny of *Larix* shows only a quantitative difference in its

early sequence from the extreme type of cleavage found in pine, and hence the type in *Larix* is designated as *delayed cleavage polyembryony*.

In development of the massive embryo, a number of different tissues are recognized. Thirteen different tissues may be distinguished in the mature embryo; histologically they are distinct in varying degree, since nearly all of them are highly meristematic. The most important distinctions are based on differences in their functional character. The tissues represented in early ana-stage are: suspensor, columnar tissue, pleromic centrum, and mantle. In late ana-stage and continuing in telo-stage the columnar tissue gives rise to the peri-column and periblem, the pleromic centrum gives rise to the two generative meristems above and below, to the nodal primordium, procambial strands, and medullary tissue. Cotyledons are developed largely from tissue derived from the upper margins of the pleromic centrum. The mantle becomes a dermatogen over the cotyledons and upper part of the axis, but does not differentiate on the plumule primordium. Secretory canals are differentiated both in the medullar tissue and subdermally.

Columnar tissue formed basally in the early stages of massive tissue development dominates formation of lateral tissues and contributes to the final lateral enlargement of the embryo by the periblem.

The cotyledons include the last of the tissues of the mature embryo to become differentiated. Beyond the stage of cotyledon formation most of the embryonic growth occurs by intercalation within visible tissues.

Close agreement in qualitative features throughout the *Larix* embryogeny with the sequence as known for *Pinus* provides additional evidence of the close relationship between these genera. However, *Pseudotsuga* and *Picea*, and possibly *Abies*, are more likely related closely to *Larix* than any other genera.

Polarity units of gymnosperms are functionally equivalent to the primitive spindles of vascular cryptogams; the two groups are not sufficiently comparable from this fundamental standpoint, particularly with regard to origin of the root, to permit any immediate community of phylogenetic derivation. It seems probable that the ancestral archegoniate stock became differentiated into these two groups at a very early date.

Embryology in gymnosperms altogether upholds Lang's and Bower's contention that the suspensor is a primitive embryonic organ.

Gymnosperms in a fundamental sense are monophyletic in derivation. The very great conservatism of structure in the late embryo, particularly with reference to the primary root, is most indicative of this.

A causal basis is suggested as an explanation for the divergent types of polyembryony shown by cycads on one hand and conifers on the other. This is a continuation of the idea first suggested by Chamberlain involving the inability of the zygote to segment the large egg cell following the initial nuclear division.

## BIBLIOGRAPHY

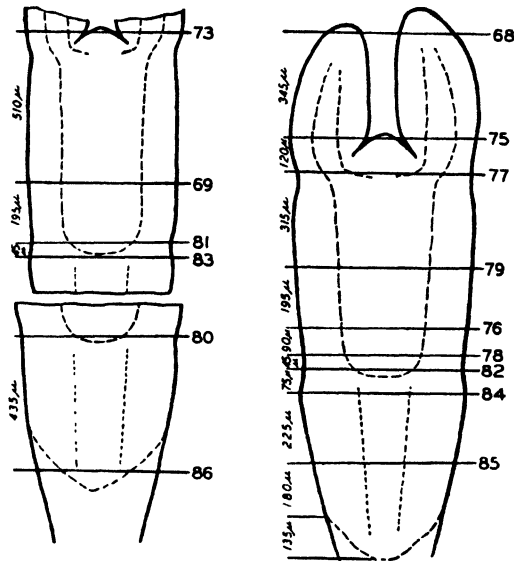
- BOWER, F. O.  
 1922. The Primitive Spindle as a Fundamental Feature in the Embryology of Plants. *Proc. Roy. Soc. Edinburgh*, 43(1):1-36.  
 1935. *Primitive Land Plants*. Macmillan, London.
- BRONGNIART, ADOLPHE  
 1881. *Recherches sur les Graines Fossiles. Silicifiées*. Imprimerie Nationale, Paris.
- BROWN, R.  
 1844. On the Plurality and Development of the Embryos in the Seeds of Coniferae. *Ann. Mag. Nat. Hist.* 13:368-374. (See also *Ann. des Sci. Nat.*, 2nd ser., *Botanique*, 1843, 20:193-199.)
- BUCHHOLZ, J. T.  
 1918. Suspensor and Early Embryo of Pinus. *Bot. Gaz.* 66:185-228.  
 1919. Studies Concerning the Evolutionary Status of Polycotyledony. *Am. J. Bot.* 6:106-119.  
 1920a. Polyembryony among Abietineae. *Bot. Gaz.* 69:153-167.  
 1920b. Embryo Development and Polyembryony in Relation to the Phylogeny of Conifers. *Am. J. Bot.* 72:125-145.  
 1925. The Embryogeny of *Cephalotaxus fortunei*. *Bull. Torr. Bot. Club*, 52:311-24.  
 1926. Origin of Cleavage Polyembryony in Conifers. *Bot. Gaz.* 81:55-71.  
 1929. The Embryogeny of the Conifers. *Proc. Int. Cong. Plant Sciences*, Ithaca, New York, 1926, 1:359-392.  
 1931a. The Pine Embryo and the Embryos of Related Genera. *Trans. Ill. Acad. Sci.* 23:117-125.  
 1931b. The Suspensor of Sciadopitys. *Bot. Gaz.* 92:243-262.  
 1936. Embryogeny of Species of Podocarpus of the Subgenus Stachycarpus. *Bot. Gaz.* 98:135-146.  
 1938. Dissection, Staining, and Mounting of the Embryos of Conifers. *Stain Technology*, 13:59-64.  
 1939a. The Embryology of *Sequoia sempervirens*, with a Comparison of the Sequoias. *Am. J. Bot.* 26:248-257.  
 1939b. The Generic Segregation of the Sequoias. *Am. J. Bot.* 26:535-538.  
 1940a. The Embryology of Cunninghamia. *Am. J. Bot.* 27:877-883.  
 1940b. The Embryogeny of Torreya, with a Note on Austrotaxus. *Bull. Torr. Bot. Club*, 67:731-754.  
 1941. Embryogeny of the Podocarpaceae. *Bot. Gaz.* 103:1-37.  
 1942. A Comparison of the Embryogeny of Picea and Abies. *Madroño*, 6:156-167.
- BUCHHOLZ, J. T., and OLD, EDNA M.  
 1933. The Anatomy of the Embryo of Cedrus in the Dormant Stage. *Am. J. Bot.* 20:35-44.
- BURRILL, T. J., and McLUER, G. W.  
 1893. The Forest Tree Plantation. *Ill. Agr. Exp. Sta. Bull.* 26:2:205-244.
- BUTTS, D., and BUCHHOLZ, J. T.  
 1940. Cotyledon Numbers in Conifers. *Trans. Ill. Acad. Sci.* 33:58-62.
- CHAMBERLAIN, C. J.  
 1919. *The Living Cycads*. University of Chicago Press.  
 1934. *Methods in Plant Histology*. (5th ed.). University of Chicago Press.  
 1935. *Gymnosperms—Structure and Evolution*. University of Chicago Press.
- CHAVEAUD, M. G.  
 1903a. Un Nouvel Appareil Secreteur chez les Coniferes. *Compt. Rend. Acad. Sci.* 136:1093-1094.  
 1903b. Disposition du Nouvel Appareil Secreteur dans le Cedre de l'Himalaya (*Cedrus deodara*). *Bull. du Mus. d'Hist. Nat.* 9:243-250.  
 1904. Transformations du Nouvel Appareil Secreteur des Coniferes. *Compt. Rend. Acad. Sci.* 139:881-883.

- COULTER, J. M., and CHAMBERLAIN, C. J.  
1917. Morphology of Gymnosperms. (4th printing, 1928). University of Chicago Press.
- DARROW, B. S.  
1936. A Fossil Araucarian Embryo. Bot. Gaz. 98:328-337.
- DOYLE, J.  
1918. Observations on the Morphology of *Larix leptolepis*. Sci. Proc. Roy. Dublin Soc. 15:310-330.  
1925. An Old Record of the Ovule of Larix. Ann. Bot. 39:209.  
1926. The Ovule of Larix and Pseudotsuga. Proc. Roy. Irish Acad. 37:170-180.
- DOYLE, J., and LOOBY, W. J.  
1939. Embryogeny in Saxegothea and Its Relation to Other Podocarps. Sci. Proc. Roy. Dublin Soc. 21:127-147.
- DOYLE, J., and O'LEARY, MARY  
1935. Pollination in Tsuga, Cedrus, Pseudotsuga, and Larix. Sci. Proc. Roy. Dublin Soc. 21:191-204.
- FOSTER, A. S.  
1940. Further Studies on Zonal Structure and Growth of the Shoot Apex of *Cycas revoluta* Thunb. Am. J. Bot. 27:487-501.  
1942. Practical Plant Anatomy. Van Nostrand, New York.
- GILEZNOFF, N.  
1849. Sur l'Embryogenie du Mélèze. Bull. Soc. Imp. Natural. Moscow, 22:566-605.
- GOEBEL, K.  
1933. Organographie der Pflanzen. (3rd ed.). Vol. 3.
- HANES, C. S.  
1927. Resin Canals in Seedling Conifers. J. Linn. Soc. London, Botany, 47:613-636.
- HOFMEISTER, W.  
1850. Review of Geleznoff (1849). Flora, 43:685-686  
1862. On the Germination, Development, and Fructification of the Higher Cryptogamia and on the Fructification of the Coniferae. (English translation by F. Currey). Ray Soc. Publ. No. 22, London.
- HUTCHINSON, A. H.  
1917. Morphology of *Keteleeria fortunei*. Bot. Gaz. 63:124-134.  
1924. Embryogeny of Abies. Bot. Gaz. 77:280-289.
- JEFFREY, E. C.  
1904. The Comparative Anatomy of the Coniferales. II. The Abietineae. Mem. Boston Soc. Nat. Hist. 6.
- LAND, W. J. G.  
1923. A Suspensor in Angiopteris. Bot. Gaz. 75:421-425.
- LANG, W. H.  
1909. A Theory of Alternation of Generations in Archegoniate Plants Based upon the Ontogeny. New Phyt. 8:1-12. (See also Discussion: New Phyt. 8:104-116.)  
1915. Presidential Address. Rept. Brit. Assn. Adv. Sci., Manchester, 1915: 701-718.
- LAWSON, A. A.  
1909. The Gametophyte and Embryo of *Pseudotsuga douglasii*. Ann. Bot. 23:163-180.
- MESSERI, ALBINA  
1935. Ricerche sulla Morfologia della Plantula nelle Coniferae; le Pinaceae. Nuovo Giornale Botanico Italiano, 42(2):267-363.
- MILHONE, D. W.  
1933. The Anatomy of the Embryo of Podocarpus. Master's Thesis (Manuscript), University of Illinois.

- OSTENFELD, C. H., and LARSEN, C. S.  
1930. The Species of the Genus *Larix* and Their Geographical Distribution. Danske Videnskabernes Selskab. Biologiske Meddelelser, 9(2):1-107.
- PENHALLOW, D. P.  
1904. Anatomy of North American Coniferales, Together with Certain Exotic Species from Japan and Australia. Am. Nat. 38:243-273, 331-359, 523-554, 691-723.
- PILGER, R.  
1926. Gymnospermae. In Engler and Prantl's Die Naturlichen Pflanzenfamilien, 2nd ed., Vol. 13. Wilhelm Engelmann, Leipzig.
- PRIESTLEY, J. H.  
1928. The Meristematic Tissues of the Plant. Biol. Rev. 3:1-20.
- REHDER, ALFRED  
1940. Manual of Cultivated Trees and Shrubs. New York.
- SAXTON, W. T.  
1930. Notes on Conifers. III. Further Points in the Morphology of *Larix europaea*. Ann. Bot. 44:161-165.
- SCHACHT, H.  
1850. Entwicklungs-Geschichte des Pflanzen-Embryon. Amsterdam.
- SCHNARF, K.  
1933. Embryologie der Gymnospermern. Linsbauer's Handbuch der Pflanzen-anatomie (Lieferung 30), II Abt., 2 Teil: Archegoniaten, Band X/2. Berlin.
- SCHÜEPP, OTTO  
1926. Meristeme. Linsbauer's Handbuch der Pflanzenanatomie (Lieferung 16), I Abt., 2 Teil: Histologie, Band IV. Berlin.
- SMITH, G. M.  
1938. Cryptogamic Botany, Vol. II, Bryophytes and Pteridophytes. New York.
- STOPES, M. C., and FUGIE, K.  
1906. The Nutritive Relations of the Surrounding Tissues to the Archegonia in Gymnosperms. Beihefte zum Bot. Centralbl 20(pt.1):1-24.
- STOVER, E. L.  
1928. A Method of Staining Microscope Slides for Beginning Students. Trans Ill. Acad. Sci. 21:186.
- STRASBURGER, E.  
1872. Die Coniferen und die Gnetaceen: Eine morphologische Studie. Jena.  
1879. Die Angiospermen und die Gymnospermen. Jena.
- WIELAND, G. R.  
1916. American Fossil Cycads, II, Taxonomy. Carnegie Inst. Pub. 34.
- WODEHOUSE, R. P.  
1929. The Origin of Symmetry Patterns in Pollen Grains. Bull. Torr. Bot. Club, 56:339-350.
- WOYCICKI, Z.  
1900. Befruchtungprozess bei den Coniferen (Abstract). Bot. Zeitung, 58(pt.2):39.  
1923. Einige Beobachtungen über Prothallien und Archegonien bei *Larix dahurica* Turcz. und *Larix europaea* DC. Acta Soc. Bot. Polon 1(3):149-164.

## EXPLANATION OF PLATES

As a general practice, the figures of early embryo stages are oriented with the apex downward, as if seen in the seed with the micropyle turned upwards; the figures of the late embryo are oriented with the plumule primordium upward to correspond with the later attitude assumed in germination.



In the above diagrams of parts of three of the telo-stage embryos that were sectioned transversely, the numerals at the right indicate the relative positions of sections illustrated in Figs. 68, 69, and 73 on Plate IV, Figs. 75-80 on Plate V, and Figs. 81-86 on Plate VI. Distances between sections (cut 15  $\mu$  thick) are given on the left.

## PLATE I

Fig. 48.—Longitudinal section through micropylar end of nucellus and gametophyte. Two germinated pollen grains are on the truncated tip of the nucellus with straight pollen tubes penetrating toward the archegonia. Fertilization has occurred, but the zygotes do not show in this section. Collection of May 21, 1933.

Fig. 49.—Transverse section of gametophyte showing proembryos in two of the five archegonia. Proembryo cells shown are of the suspensor and rosette tiers; the transverse walls between them are cut on a slant due to inclination of the walls. Collection of May 26, 1933.

Fig. 50.—Transverse section (taken just below that in Fig. 49) showing the apical tier of the proembryos. Two of the vertical rows facing each other across the short diameter of the archegonium meet at a straight central wall, whereas the two rows in line with the longer archegonial diameter do not touch each other. This shows best in the proembryo on the left.

Fig. 51.—Transverse section through four unfertilized archegonia in the gametophyte. The spiral fibrillar character of the cytoplasm is noteworthy, although it has been exaggerated by imperfect fixation. Same collection as Fig. 49.

Fig. 52.—Transverse section of gametophyte through four recently fertilized archegonia, showing extremely irregular nuclear membranes. Same collection as Fig. 49.

Fig. 53.—Transverse section through the lower ends of archegonia with free nuclei of proembryo. Same collection as Fig. 49.

Fig. 54.—Uppermost archegonium in Fig. 53 at greater magnification (about 300 times). Note the asymmetrical arrangement of free nuclei.

Fig. 55.—Longitudinal section of an early ana-stage embryo, showing at its tip the last vestige of a tetrahedral apical initial. Persistence of the apical initial may be correlated with the more than usually conical shape of the embryo tip. Collection of June 4, 1933.

Fig. 56.—Longitudinal section of an early ana-stage embryo, showing a repressed embryo (polarity unit) with a stage II apical cell still associated with it at the right. The apical initial has been completely eliminated in the dominant embryo. Same collection as Fig. 55.

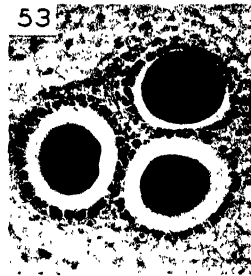
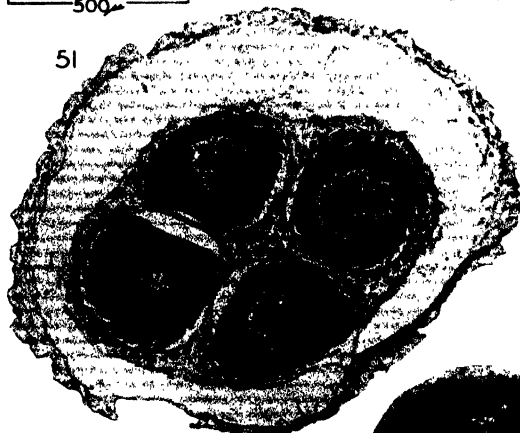
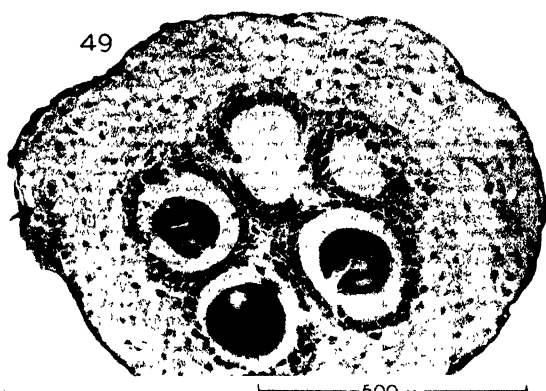
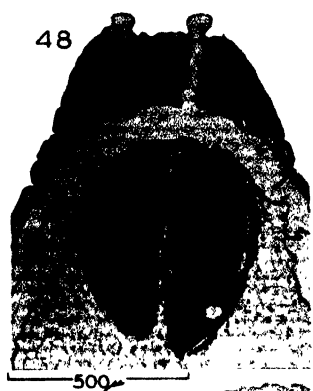


PLATE I

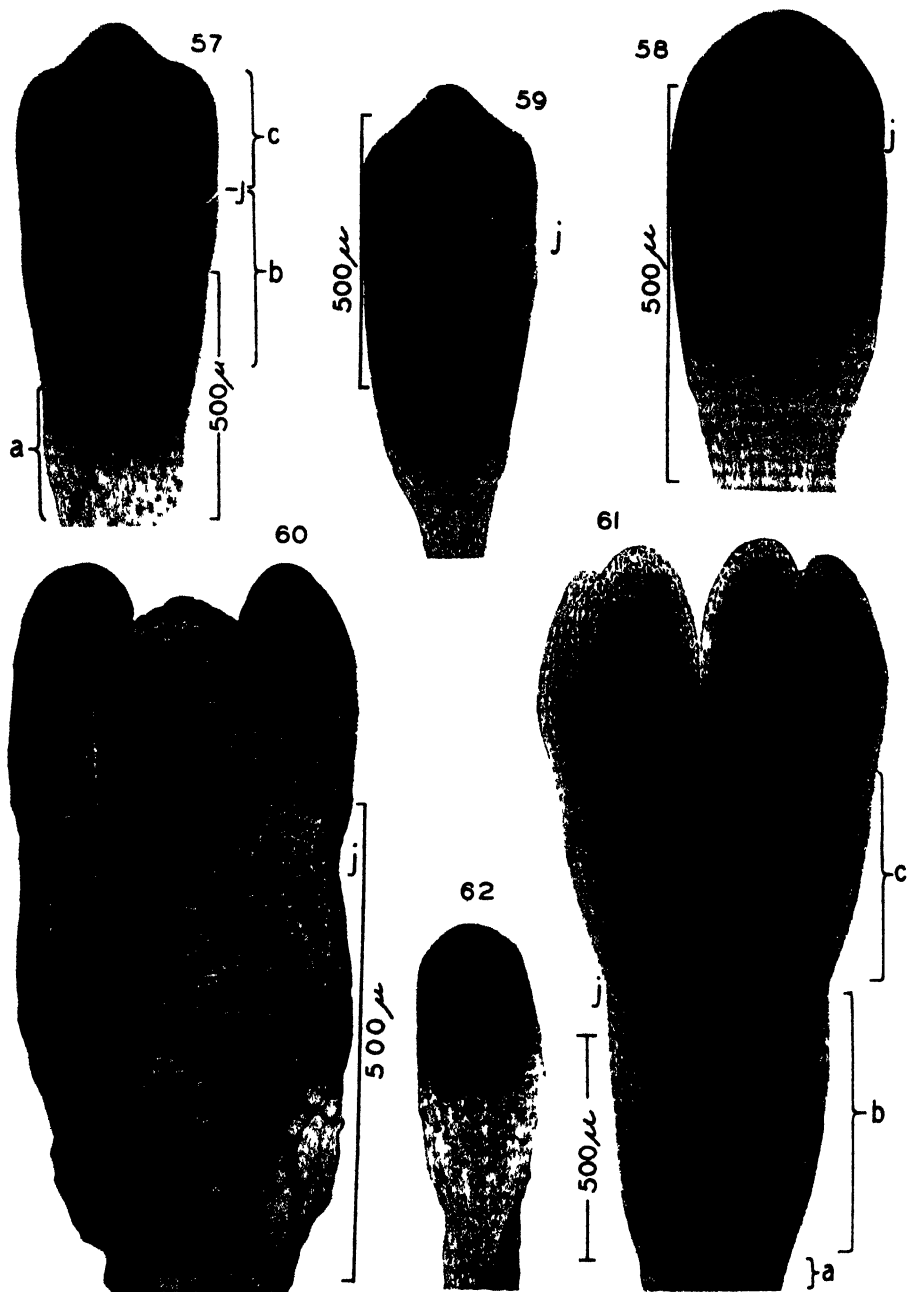


PLATE II

## PLATE II

Letters indicate parts: *a*, cells contributing to suspensor;  
*b*, calyptroperiblem; *c*, axis; *j*, juncture zone.

Fig. 57.—Whole embryo in late ana-stage, stained with phloxine. Collection of June 16, 1932.

Fig. 58.—Whole embryo in late ana-stage, stained with phloxine. Area of the pleromic centrum is indicated. Same collection as Fig. 57.

Fig. 59.—Whole embryo in late ana-stage. The plumule primordium here shows its greatest prominence. Area of the pleromic centrum is indicated. Same collection as Fig. 57.

Fig. 60.—Median longitudinal section of embryo in early telo-stage. All tissues except secretory elements have made their appearance. Collection of June 25, 1932.

Fig. 61.—Whole embryo in late telo-stage, stained with phloxine and slightly crushed. Cotyledons are about two-thirds grown, and the axis will continue to elongate about one-fourth; the calyptroperiblem is nearly mature in size. Total length 1.63 mm.; length of cotyledons 480 microns (beyond the node), axis about 600 microns, calyptroperiblem about 550 microns. Most of the suspensor is badly collapsed. Same collection as Fig. 60.

Fig. 62.—Whole embryo in mid-ana-stage, stained with phloxine, photographed at the same magnification as Fig. 61 for comparison. The addition of lateral tissues (pericolumn and periblem) has hardly begun; columnar tissue occupies the lower two-thirds of the non-vacuolate tip. Same collections as Fig. 57.

## PLATE III

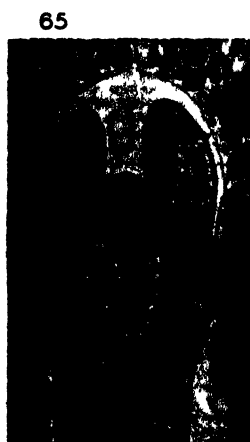
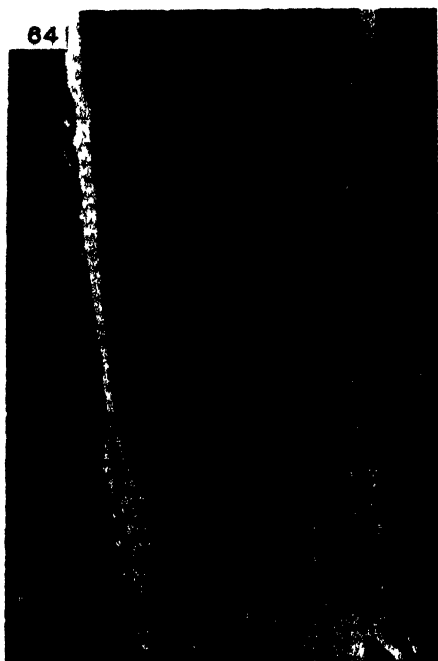
Fig. 63.—Median longitudinal section of late telo-stage embryo within gametophyte. The seed coat has been removed; some vestiges of the nucellus remain. The megaspore membrane is visible around the gametophyte at the upper end of the figure. Collection of June 25, 1933.

Fig. 64.—Median longitudinal section of calyptroperiblem of late telo-stage embryo. Column is about 520 microns long; embryo 345 microns in diameter at the juncture zone. Same collection as Fig. 63.

Fig. 65.—Longitudinal section of telo-stage embryo showing pleromic secretory elements. Same collection as Fig. 63.

Fig. 66.—Longitudinal section of embryo similar to Fig. 65. Total length 1.25 mm. Same collection as Fig. 63.

Fig. 67.—Longitudinal section of seedling about two days after germination. Only the seed coat was removed before sectioning. The cotyledons have expanded about one-third from the resting condition and measure a little over a millimeter in length. The axis still within the seed has broadened to about 650 microns. The plumule primordium has enlarged somewhat. (Two of the earliest primordia for primary leaves were discernible in another section.) A few xylem elements have been established in the upper part of the seedling; those first appearing are short and scalariform in the angles of the cotyledonary node. Pleromic secretory elements extend the length of the radicle; the subdermal elements are limited to the hypocotyl and the cotyledons. Not only has the suspensor been destroyed in germination, but the dermal layers of the lower portion of the radicle are being sloughed off. Thus far, the food supply for embryo growth has come from the region at the rear of the gametophyte, where the cotyledons have enlarged and been in contact with the food reserve. The dermal absorption of food is probably the last of the purely embryonic functions to be outgrown by the seedling, and when the outer layer of these regions ceases to be absorptive, all the requirements for holophytic nutrition are present.



500  $\mu$

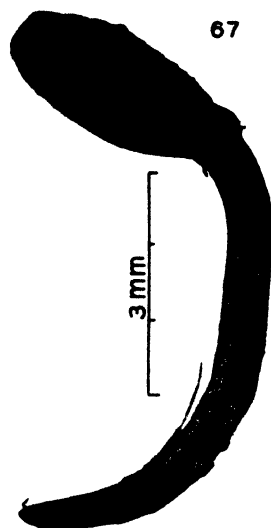
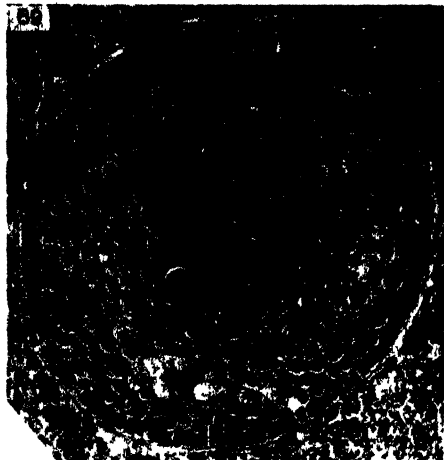
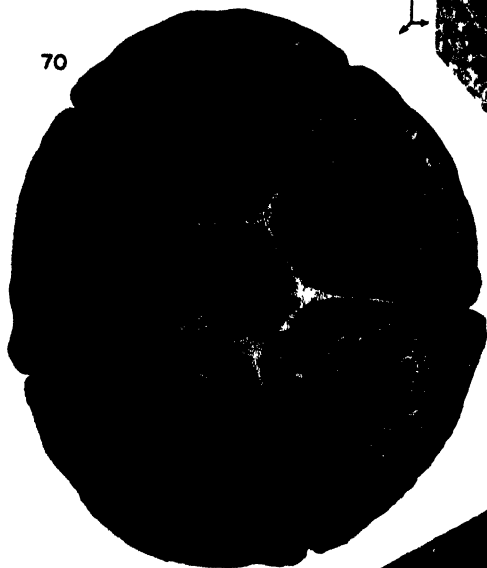


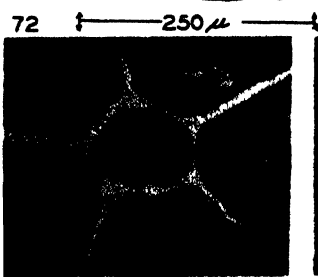
PLATE III



70



250 μ



72

250 μ



73

74

250 μ



PLATE IV

## PLATE IV

(Figs. 68-74 are from the collection of June 25, 1933.)

(For location of sections, see diagram on page 85.)

Fig. 68.—Transverse section of cotyledon tips in telo-stage embryo. The difference in cotyledon length is real and not due to obliquity of the section.

Fig. 69.—Transverse section of lower portion of plerome in telo-stage embryo. About ten pleromic and thirty subdermal secretory elements are present.

Fig. 70.—Transverse section of telo-stage embryo showing the plumule apex and basal part of cotyledons with cotyledonary procambia.

Fig. 71.—Longitudinal section of telo-stage plumule primordium. Note lack of epidermis and relative size of tip cells.

Figs. 72, 73, 74.—Transverse sections of telo-stage plumule primordia. Note variation in arrangement of tip cells. Thickness of the sections (15 microns) is indicated by the strip of displaced megaspore membrane lying diagonally across the section in Fig. 73.

## PLATE V

(Figs. 75-80 are from the collection of June 25, 1933.)

(For location of sections, see diagram on page 85.)

Fig. 75.—Transverse section of telo-stage embryo showing plumule apex and basal parts of cotyledons. Subdermal secretory elements on the two lower cotyledons have been outlined; they are restricted to the abaxial surfaces. The two cotyledons at the upper right correspond to the two short cotyledons in Fig. 68, both sections being from the same embryo.

Fig. 76.—Transverse section of lower part of axis of telo-stage embryo, about 150 microns above the base of the plerome and 195 microns below the level of the section shown in Fig. 79. Pleromic and subdermal secretory elements have been outlined.

Fig. 77.—Transverse section just above nodal primordium of telo-stage embryo and about 120 microns below the level of the section shown in Fig. 75. Subdermal secretory elements in the lower part of the photograph have been outlined; about thirty-six such elements in all are present.

Fig. 78.—Transverse section near base of axis of telo-stage embryo, about 90 microns below the level of Fig. 76. Subdermal secretory elements are absent, but pleromic elements are present (indicated by solid black).

Fig. 79.—Transverse section of telo-stage embryo about the middle of the axis and about 315 microns below the level of Fig. 77. Subdermal secretory elements, which show to advantage in this photograph, are untouched. Pleromic elements have been outlined.

Fig. 80.—Transverse section of telo-stage embryo which appears to include the base of the plerome. The ends of pleromic secretory elements are present in the second section above this one, and the column is distinct in the fourth section below it.

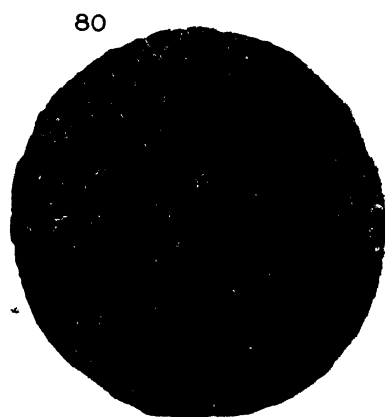
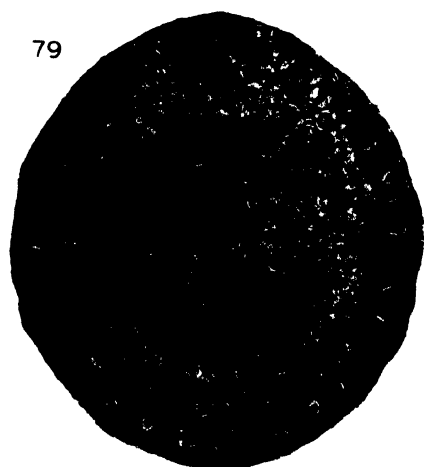
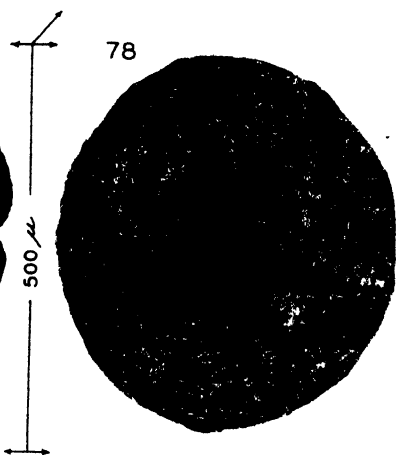
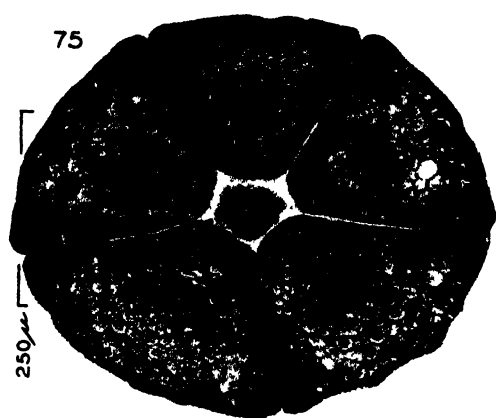
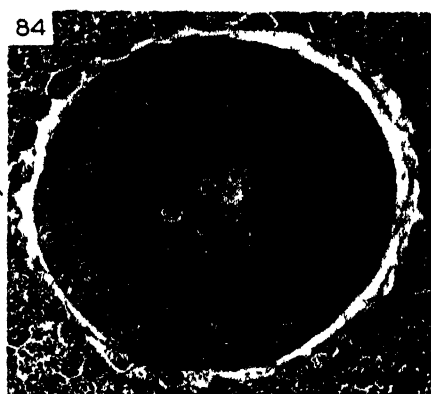
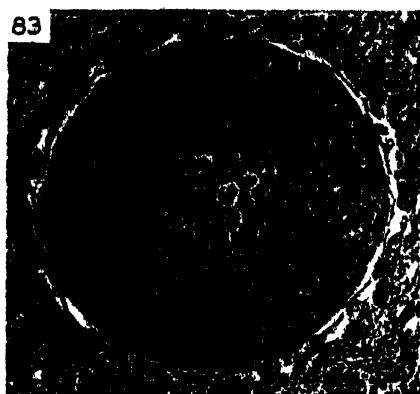
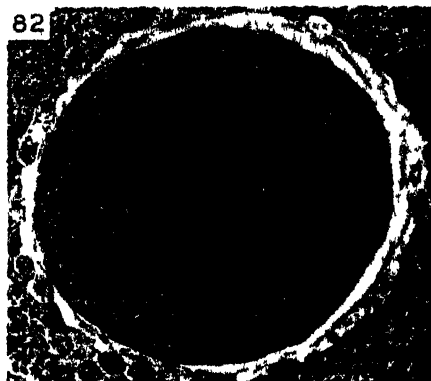
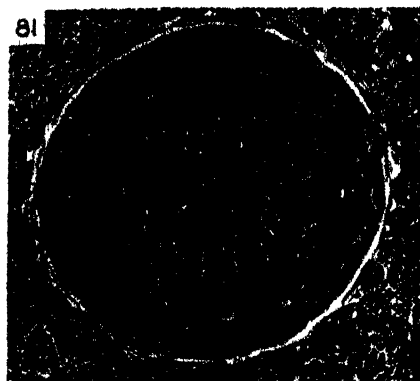
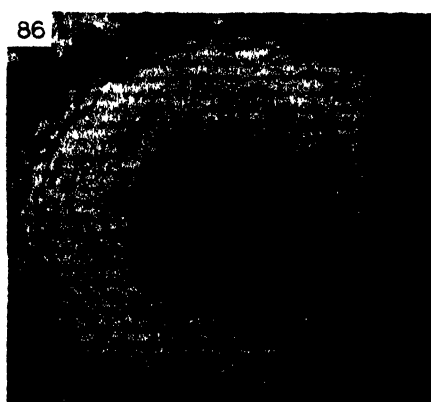
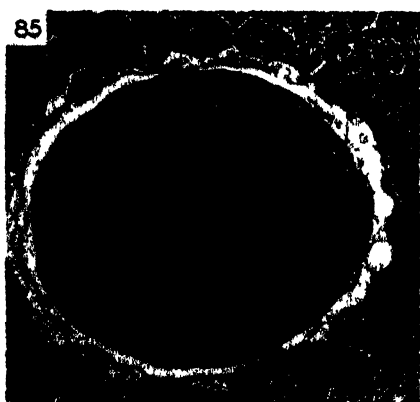


PLATE V



500 μ



## PLATE VI

(Figs. 81-86 are from the collection of June 25, 1933.)

(For location of sections, see diagram on page 85.)

Fig. 81.—Transverse section of telo-stage embryo just above the base of the plerome and about 195 microns below the level of Fig. 69. Compare Figs. 69, 78, 80, 82, and 83, all representing sections in the lower axial part of the embryo.

Fig. 82.—Transverse section of telo-stage embryo at the base of the plerome and about 45 microns below the level of Fig. 78. The juncture zone is at about this level.

Fig. 83.—Transverse section of telo-stage embryo at the uppermost part of the column below the initial cells at the base of the plerome. This section is about 45 microns below that shown in Fig. 81.

Fig. 84.—Transverse section of telo-stage embryo in the upper part of the column, about 75 microns below the level of Fig. 82.

Fig. 85.—Transverse section through the middle of the telo-stage calyptroperiblem, about 225 microns below the level of Fig. 84. The suspensor is wholly vacuolate about 320 microns below this level.

Fig. 86.—Transverse section across the extreme base of telo-stage calyptroperiblem with marginal (suspensor) cells enlarged and vacuolate. This section is about 435 microns below that shown in Fig. 80.



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